Comparative studies on Cerastoderma edule (L.) and Cerastoderma glaucum (Poiret).

Boyden, Charles Richard

COMPARATIVE STUDIES ON CERASTODERMA EDULE (L.)

AND CERASTODERMA GLAUCUM (POIRET).

by

Charles Richard Boyden.

Department of Zoology & Comparative Physiology,
Queen Mary College,
Mile End Road,
London, E.1.

Thesis submitted for the degree of Doctor of Philosophy.

September, 1970.

ABSTRACT

Comparative investigations of many aspects of the biology of the cockles Cerastoderma edule (L.) and Cerastoderma glaucum (Poiret) have been conducted.

The nomenclature and systematic status of the two cockles has been reviewed.

The distribution of C.edule and C.glaucum in the British Isles has been investigated. Field studies were conducted to determine:

(1) validity of the morphological characters previously used to separate the two cockle types.

(2) the relationship between adjacent populations of the two cockles and (3) habitat preferences of the cockles.

A mixed population of C.edule and C.glaucum from the estuary of the River Crouch, Essex, has been examined from a comparative standpoint.

The demographic properties, shore distribution and shell-ribbing of the Crouch Cerastoderma populations have been investigated. A study of the reproductive cycles of the Crouch cockles has established that in two seasons 1968 and 1969, C.edule spawned seven weeks' earlier than C.glaucum. This factor explains how the two genetic types are maintained within a common environment. An investigation into the symbiont fauna of the cockles also lends support to the specific separation between C.edule and C.glaucum.

A difference has been shown in the behaviour of the two cockles in air; C.edule breaths air during aerial exposure. The lower survival of C.glaucum in air compared with C.edule is suggested to be one factor accounting for the absence of this cockle from high shore levels.

It was observed that the digestive gland colouration differed in the two cockles; being black in C.glaucum, but variably coloured in C.edule. Spectrophotometric analysis of acetone extracts of the digestive gland was conducted in an attempt to establish the cause of this difference. A polar carotenoid has been discovered to be abundant in the digestive gland of C.glaucum. The lipids of the digestive gland and magnesium content of the shell have also been investigated.

The relationship between the two cockles is concluded to be at a specific level.

ACKNOWLEDGEMENTS

It is a pleasure to thank:

The Science Research Council: for sponsoring this investigation.

Professor K. Simkiss: within whose Department this study was conducted.

Dr. G.B. Williams: for constructive criticism and advice.

Dr. R.C. Newell and Dr. M. Walkey: for generous advice.

Messrs. M.J. Daniel, H.J.G. Dartnall and I.C. White: for helpful discussion and encouragement.

and The Technicians at Queen Mary College for their excellent technical assistance.

Also deserving my thanks are my parents for their tolerance and encouragement; and I would like to acknowledge most sincerely the help given so freely by my friends - Misses P. Wheeler, G. Wright, A. Carter, C. Sexton and J. Berry - in typing this thesis. My thanks especially to Pam.

LIST OF CONTENTS

	Page number
ABSTRACT	1
ACKNOWLEDGEMENTS	3
CONTENTS	4
INTRODUCTION	9
SECTION I: Nomenclature of the cockles studied in this research.	13
SECTION II: Use of morphological shell characteristics to separate the British Cerastoderma.	26
1. Relationship of ligament length to shell breadth in various cockle populations.	29
(a) Arithmetric plots.	29
(b) Logarithmic plotting of ligament length/shell breadth data.	38
2. An attempt to quantify the posterior elongation of the shell of C. glaucum compared with C. edule.	55
3. Internal colouration of the shell of the two Cerastoderma.	61
SECTION III: Distribution of the cockles C. edule and C. glaucum in the British Isles.	64
1. Distribution of Cerastoderma edule (L).	65
2. Distribution of Cerastoderma glaucum (Poiret).	67
SECTION IV: Field investigations to determine habitat and distribution of C. edule and C. glaucum.	73
1. Field studies in south-east England.	74
(a) Cockle populations of the Cerastoderma edule type only.	75
(b) Cockle populations of both Cerastoderma types.	75

(i) The distribution of Cerastoderma edule and Cerastoderma glaucum in the neighbourhood of the Crouch and Roach estuaries, Essex. 77

(ii) Geological explanation for the presence of C. glaucum in the Crouch and Roach estuaries. 78

(iii) Description of the two mixed cockle populations in the Crouch and Roach estuaries. 82

(c) Cockle populations of the Cerastoderma glaucum type only. 87

(i) North Norfolk. 87

(ii) Suffolk. 87

(iii) Essex. 88

(iv) Kent. 91

(v) Sussex. 92

(vi) Hampshire. 94

(vii) Isle of Wight. 97

(viii) Dorset. 97

2. Field work to determine the distribution of Cerastoderma glaucum (Poiret) elsewhere in the British Isles. 100

(a) South Wales. 100

(b) Field study of south-eastern Eire. 101

(c) Field study of western and south-western Eire. 102

(i) Trawnagh, Kinvarra Bay, Co. Galway. 102

(ii) Finavarra, Kinvarra Bay, Co. Galway. 103

(iii) Aughinish, Kinvarra Bay, Co. Galway. 103

(iv) Salt lake, Clifden, Co. Galway. 104

(v) Curhawnagh loch, Nr. Clifden, Co. Galway. 105

(vi) Unmarked lagoon nr. Ballyconneely, Co. Galway. 105

(vii) Loch at Keeraunnagark, Co. Galway. 105

(viii) Chapletown, Nr. Tralee, Co. Kerry. 105

(ix) Unmarked lagoon at Rosscarbery, Co. Cork. 106

(d) Discussion of field investigations. 108

(i) Salinity tolerances. 108

(ii) Conclusions on ecology and theories concerning distribution of C. glaucum. 113

SECTION V: Comparative studies on the mixed Cerastoderma populations of the Crouch and Roach estuaries together with some reference to various single cockle populations. 132

1. Demographic properties of the Crouch mixed population. 133

(a) Annual rings, disturbance rings and age structure of the Crouch cockle populations. 133

(b) Comparison of sizes of C. edule and C. glaucum from the Crouch mixed population. 140

(i) Length to age relationship of Crouch C. edule compared with values available for C. edule in the literature. 142

(ii) Comparison of shell size with age for the two cockle types. 142

(iii) Average growth increments of the two cockles over successive years. 148

2. Shore distribution of the two members of the Cerastoderma. 152

3. Distribution of rib number in various cockle populations. 157

(a) Measurement of rib-number. 158

(b) Factors affecting rib-number. 159

(c) The effect of substrate upon rib-number. 159

(d) Distribution of rib-numbers in the Crouch and Roach mixed cockle populations. 160

(e) Distribution of rib-number in single cockle populations. 168

(f) Relationship of rib-number to salinity in single cockle populations. 174

(i) Cerastoderma edule. 174

(ii) Cerastoderma glaucum. 178

(g) Conclusions concerning salinity tolerances of the Cerastoderma. 183

4. Shell weight of cockles from the mixed Crouch population. 185

5. Comparison of tissue weights in the Crouch Cerastoderma. 187

SECTION VI: A comparative analysis of the reproductive cycles of the cockles Cerastoderma edule (L.) and Cerastoderma glaucum (Poiret). 196

SECTION VII: A comparative investigation into the Symbiont fauna of the cockles Cerastoderma edule (L.) and Cerastoderma glaucum (Poiret). 249

SECTION VIII: The behaviour, survival and respiration of the cockles Cerastoderma edule (L.) and Cerastoderma glaucum (Poiret) in air. 317

SECTION IX: Comparative biochemical studies between the cockles Cerastoderma edule (L.) and Cerastoderma glaucum (Poiret) 372

1. Spectrophotometric analysis of acetone extracts of the digestive gland of the two Cerastoderma. 373

2. Determination of total fat content of the digestive glands of C. edule and C. glaucum. 390

3. Thin-layer chromatography of the digestive gland lipids of C. edule and C. glaucum from the Crouch mixed population. 395

4. Separation of carotenoid pigments from the digestive glands of C. edule and C. glaucum. 403

5. Chemical investigation into the nature of the polar xanthophyll of Cerastoderma glaucum. 412

6. Additional biochemical investigation into the magnesium content of the shells C. edule and C. glaucum. 419

GENERAL CONCLUSIONS 430

APPENDIX I - British Museum (Natural History section) specimens. 433

APPENDIX II - A. Legend for distribution of Cerastoderma edule L. around the British Isles. 436

B. Legend for distribution of Cerastoderma glaucum (Poiret) around the British Isles. 439

APPENDIX III - Localities visited in Eire other than C. glaucum sites. 440

APPENDIX IV - Incidence of a gymnophallid in the Crouch cockles. 442

APPENDIX V - Comparison of Cercaria mytae (Uzmann, 1952) and Heiogymnophallus minutus (Cabbold, 1859). 443

APPENDIX VI - Statistical analyses used in this investigation. 446

INTRODUCTION

Morphological differences have long been used as the most convenient method of establishing species differentiation. By so doing it was assumed that reproductive isolation and morphological differences evolve together, an assumption which is not always correct when intra-specific variations are considered. For example, some sympatric populations which may not always be morphologically distinct, nevertheless exhibit other differences such as biochemical (Hanwell, 1966), reproductive or behavioural which warrant regarding the two forms as separate species. Such sibling species, (Mayr, 1942), because of morphological similarity have previously been overlooked and have only been discovered through differences in habitat, ecology or physiology.

Biological isolation of populations is a necessary requirement if the divergence leading to the formation of separate species is to take place. Organisms occur in populations of interbreeding, non-identical individuals which constitutes the variation within a species. When populations cease to breed with neighbouring populations accumulation of inheritable variations can take place in divergent directions. Thus differences become intensified and upon later convergence, in overlapping populations, these differences could preclude any interbreeding, indicating the attainment of specific differentiation. It is therefore not the variation between populations that is important in the species concept, it is the non-interbreeding of natural populations which is the decisive species criterion. (Mayr, 1963).

Various appraisals of the species concept have been suggested which explain the border-line cases where separation does not appear to be quite complete. Some discontinuous populations potentially can interbreed, but to retain their identity, cannot exist at the same place at the same time, (sympatric and Synchronous). However, under certain circumstances mixed populations may occur. Dobzhansky (1950) defined the species as "the reproductive community of sexual and cross-fertilising individuals which share in a given gene pool", whilst Mayr (1940) phrased a similar definition as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". Thus a good criterion of specific status is the sympatric and synchronous co-existence of natural populations without interbreeding. (Mayr, 1946). This concept is definite and requires reproductive isolation as its objective for maintenance.

The attainment of specific status depends upon the degree of differences between two close relatives. Evolution is a gradual process, thus populations in nature occur which have not quite achieved a species separation, having acquired some attributes of distinct species but lacking others. The isolating mechanisms between two populations are built up step by step, thus most isolating mechanisms of an incipient species may be imperfect or incomplete. The species relationship is reached when the process of speciation has become irreversible, and isolation is effective even in sympatric populations.

The species category is by no means the lowest taxonomic unit, although the value of species sub-divisions is debatable, because of their

somewhat imprecise nature. The term variety, used extensively by early taxonomists, has gradually been substituted by more definite terminology. Thus variety has been used to cover both variant individuals and variable populations. As early as 1904 Rothschild, Hartert and Jordan advocated the use of the word aberration to denote individual variation and sub-species for geographical forms which cannot rank as full species. However, the use of variety or races to describe extremes of individual variation is still a very useful concept on a localised level. Local populations or demes may differ morphologically from the "type" species, but nevertheless are still members of that one species. Mayr (1957) defines the sub-species as an aggregate of local population of a species inhabiting a geographical sub-division of the range of the species and differing taxonomically from other populations of the species. A wide distribution of the "sub-species" with uniformity of the morphological, ecological, behavioural, and physiological characters, and a method of reproductive isolation from other populations of the species must elevate the "sub-species" to a specific level. Thus the sub-divisions of a species depends upon the extent and uniformity of the differences within that species.

It is therefore generally recognised that the concept of a morphologically defined species is unsatisfactory as it recognises only a small selection of the many adaptations which animals exhibit to the environment. This approach has given way to a method of enquiry which involved comparative studies in ecology, behaviour, physiology and biochemistry. In this investigation this latter type of approach has been conducted to clarify the true systematic relationship between two closely related cockles.

The thesis presented here has been divided into several distinct sections. The nomenclature and morphological separation between the two cockles is considered in the first two sections. Extensive field-work which has been conducted in south-east England and Eire to determine the habitat preferences and distribution of the two cockles is discussed in Sections III and IV. Various comparative studies mainly on cockles collected from the mixed populations of the Crouch and Roach are recorded in Section V. An investigation to determine the presence of reproductive isolation in the mixed population and the symbiont fauna of the two cockles is considered in the subsequent two sections. A comparative study into the physiology of the cockles in relation to aerial exposure is recorded in Section VIII, and finally the last section is made up of an assortment of comparative biochemical investigations. An attempt has been made to make each section as independent as possible, which has resulted in some unavoidable duplication concerning several aspects of the study and for which I apologise in advance.

References

DOBZHANSKY. Th., 1950. Mendelian populations and their evolution. Amer. Nat. Vol. 84. pp. 401-418.

MAYR, E., 1940. Speciation phenomena in birds. Amer. Nat. Vol. 74, pp. 249-278

MAYR, E., 1942. Systematics and the origin of species. Columbia Univ. Press, N.Y

MAYR, E., 1957. Species concepts and definitions. In E. Mayr, ed. 'The Species Problem'. Amer. Assoc. Adv. Sci. Publ. No. 50. pp 1-22.

MAYR, E., 1963. 'Animal Species and Evolution'. Belknap press of Harvard Univ. Press Cambridge, Massachusetts.

MANWELL, C., 1966. Sea cucumber sibling species: polypeptide chain types and oxygen equilibration of hemaglobin. Science, vol.152, pp.1393-6.

ROTHSCHILD, W., HARTERT, E., and JORDAN, K., 1894. Note by the editors in Novit. Zool. Vol. I, p. 1.

SECTION - 1

SECTION I

NOMENCLATURE AND SYSTEMATIC RELATIONSHIPS

The nomenclature, concerning the cockles used in this research, has been extremely confused since the time of Linneus. Two morphological cockle types, called here for convenience edule and glaucum, are recognised as extremely close relatives.

The common cockle, edule, is well known, but, in recent literature, the naming of this cockle has become confused as two generic names have been supported. Thus some authorities (Tebble, 1966; Bowden & Hoppell, 1968; Glemarec, 1968) adopt the generic name Ceractoderma (Poli); whilst others (Høpner-Petersen, 1958, 1968; Russell, 1969), as well as the authors of more general ecological, physiological and behavioural studies: (Hancock & Urquhart, 1965; Hancock, 1967; Newell & Northcroft, 1967; Bowers & James, 1967; James and Bowers, 1967; Bowers, 1969; Horton, 1970), use the generic name Cardium (Linneus).

The very closely related cockle, glaucum, of the same genus, also occurs on the British Isles coast. Morphologically the two cockles are very similar, the most obvious differences being the posteriorly elongated shell and short valve ligament of glaucum. The other diagnostic shell morphological differences between the two can be found elsewhere, (Høpner-Petersen, 1958; Turk, 1964; Tebble, 1966).

The first problem is the selection of the correct generic name. Cardium was erected by Linneus in the Systema Naturae 10, 1758, of which the type species, as originally ascribed by Children, 1823, is the West African cockle Cardium costatum (L.) This, and related species, bear little morphological resemblance to the edule-glaucum cockles, the only relationship being that they belong to the same super-family, the Cardiacea. Because of these

differences they cannot belong to the same genus. It must be noted that the concept of type species has only originated relatively recently, thus Cardium edule, as first named by Linneus has been perpetuated through much of the nineteenth century literature (see Forbes & Hanley (1853) p. 15), but nevertheless it is not the type species of Cardium (s.s.)

The next available genus name used to describe the edule-glaucum cockles is Cerastoderma introduced by Poli in 1795. The type species for this genus is Cardium edule (L.), as designated by Martens (1870). As it is obvious that edule and glaucum are extremely close relatives, separated either at the specific or at a variety level, they must both belong to the same genera, which after elimination of Cardium, must be Cerastoderma.

** Recent publications by lamellibranch systematists, Tebble (1966), Bowden & Heppell (1968), Glemarec (1968) and Moore (1969) arrive at a similar conclusion. The Conchological Society of Great Britain also follows this nomenclature (see - Progress report on Marine Census of the Conchological Society 1969). Høpner-Petersen (1968) discussing the fauna of the Faroe's retains the usage of the genus Cardium for edule but he gives no reasons for this retention. Only Russell (1969) argues the case of retaining Cardium. However, by accepting the genus Cardium for the edule-glaucum cockles he is either systematically placing edule-glaucum close to costatum (which they are not), or he is supporting two separate genera of Cardium, which is unacceptable. Neither has he rejected the validity of the original type species of Cardium, Cardium costatum as designated by Children (1823). The use of Cerastoderma (Poli) at a 'subgeneric' level has been advocated in the literature. Adams & Adams (1858) used Cerastoderma as a section of the genus Cardium and this was followed by many others, (e.g. Roner, 1859; Fischer, 1887). Bucquoy, Dautzenberg and Dollfus (1898) support its use at the subgeneric level retaining however at the same time the genus Cardium. This was also

supported by Winckworth (1932) and followed by Turk (1964). However, Morch (1853) in the Yoldi catalogue had reintroduced Cerastoderma (Poli) at a generic level applying this to the edule-glaucum cockles. This has been followed by Coen (1915), Chavan (1945) and more recently by Kaltenbach (1962), as well as in the modern works of lamellibranch systematists mentioned previously. It is this use which is supported in this thesis.

By using the genus Cerastoderma there are no difficulties in applying affinities within the Cardiidae. In fact it separates edule and glaucum from other members of the Cardiacea, which is the main reason why Russell (1969) advocates the use of Cerastoderma at the sub-generic level. Thus it is agreed with Russell that edule-glaucum need to be separated from other cockles, but it is maintained that the most systematic way to do this is to use Cerastoderma at the generic level, as used by Tebble, (1966) and Bowden and Heppell, (1968) and not as a sub-genus of Cardium. The most natural classification is suggested to be as follows:-

Family Cardiidae.

Genus - Cardium ——— Cardium costatum (+ close relatives)

Genus Cerastoderma ——— Cerastoderma 'edule'

Cerastoderma 'glaucum'

In a recent classification of the family Cardiidae by Moore (1969), the genus Cerastoderma has been placed in the sub-family Laevicardiinae, whereas Cardium (s.s.) has been classified in the sub-family Cardiinae. Thus Cardium and Cerastoderma have been separated at the sub-family level.

The two cockles edule and glaucum have previously been assigned many specific names by various authors (see later). Edule has retained its species name since first being designated by Linneus (1758), and there is thus no problem concerning this common cockle. However, the glaucum cockle type has been referred to by a variety of synonyms. These

have been noted by Forbes & Hanley (1853 p. 18) and are listed below together with names from other authorities:-

C. rusticum Chemnitz (1782)

C. glaucum Bruguière (1789)

C. glaucum Poiret (1789) - from Pallary (1919)

C. luridum Poli (1795)

C. clodiense Renier (1804) - from Høpner-Petersen (1958)

C. lamarcki Reeve (1845) } - Equated as synonymous by Hanley (1856)
C. Celticum Reeve (1845) }

These various names have been perpetuated through the literature. Brackman (1936, 1937) used C. clodiense which has since been invalidated by Opinion 427, as has C. rusticum Chemnitz (Opinion 184), presumably because C. rusticum had previously been designated to what is now known as Acanthocardia tuberculata by Linneus in 1758. Høpner-Petersen (1958), Tebble (1966) and McMillan (1969) adher to lamarcki. However, as rusticum is not available the next species name should be glaucum (1789) which predates lamarcki Reeve (1845). The original confusion probably arose from the fact that the Mediterranean cockle had not been equated with the Baltic form. The Mediterranean glaucum has recently been shown to be synonymous with the Baltic lamarcki (Russell, 1969).

The final question is therefore to whom is glaucum attributable as it was proposed in the same year 1789 by two Frenchmen Bruguière and Poiret.

The work of Poiret (1789) was conducted during the years 1785 to 1786 when he studied the natural history of the North African Mediterranean coast. Bruguière (1789), in his study of cockles collected from the Languedoc Mediterranean coast of France, acknowledges that Poiret had discovered C. glaucum on the Algerian coast. The descriptions of this

cockle by Bruguière and Poiret are almost identical. In fact, the wording is so similar that it is obvious that one author extracted his descr ption from the other. As Bruguière was writing an Encyclopedia of Natural History it seems likely that he drew upon information supplied to him by other authorities e.g. by Poiret. It is argued by Hara (1951), and supported recently by Russell (1960):- "that more can be discovered from the description of Bruguière than from Poiret". As has already been pointed out, the shell morphology descriptions are almost identical, Bruguière adding only a few comments upon the similarity between C. glaucum and juvenile C. rusticum (L.) (=Acanthocardia tuberculata), and that C. glaucum could be C. virgineum of Linneus. The description of Bruguière is not regarded here as superior to that of Poiret, and in fact it is thought likely that Bruguière followed Poiret in his description of C. glaucum.

Although Sherborn (1850) in the Index Animalium, records C. glaucum (Poiret, 1789), he did not make a valid selection between the authors, as he does not mention C. glaucum (Bruguière, 1789). The first valid selection was made by Pallary (1919), who considered both the works of Bruguière and Poiret. He concluded by supporting Poiret as species author for C. Glaucum. This has been followed in a recent revision of the classification of British Lamellibranchs by Bowden & Keppell (1968). Thus as Poiret had previously been selected in the literature, the subsequent ascription of glaucum to Bruguière, by Hara (1951) and recently by Russell (1969), is invalid.

The nomenclature of the two cockles of this research is thus:

The common littoral cockle = Cerastoderma edule (Linneus 1758)

and the lagoon cockle = Cerastoderma glaucum (Poiret, 1789)

In this research only the cockles C. edule and C. glaucum have been considered. Bucquoy, Dautzenberg & Dollfus (1898), Winckworth (1932) and Turk (1964) include in the sub-genus Cerastoderma those 'species' which are very closely related morphologically to C. edule, i.e. C. edule (L.) and C. glaucum, (though they used different names for the latter cockle). Tebble (1966) also included only the two above cockles in the genus Cerastoderma. Bowden & Hoppell (1968), however, add another sub-genus Parvicardium (Monterosata) to the genus Cerastoderma. Whether or not this inclusion of Parvicardium into the genus Cerastoderma is valid is outside the scope of this thesis. The only members of the Cerastoderma studied here are C. edule and C. glaucum; thus when the genus Cerastoderma is considered, it will refer solely to these two cockles.

The systematic nomenclature concerning the Cerastoderma is therefore very confused and reflects the difficulty that various authors have experienced in classifying these cockles. In the majority, only local populations have previously been studied which resulted in numerous personal views concerning the relationships within the Cerastoderma.

Numerous species names had thus been attributed to the Cerastoderma. Bucquoy, Dautzenberg & Dollfus (1898) catalogued at least 17 synonyms for C. edule. The two cockle types are called here C. edule and C. glaucum for convenience and do not indicate that a specific relationship was initially assumed. All conclusions reached by previous authorities considered solely shell morphology. As has already been pointed out, morphological variations are not always good criteria upon which to base conclusions concerning species separation - (see Introduction).

Three possibilities can be found in the literature concerning the relationship between the two cockles:

1.) That there is one very variable species C. edule producing numerous 'ecotypes' as a result of the interation of various environmental parameters.

Theory supported by:

Forbes & Hanley (1853)

Bucquoy, Dautzenberg & Dollfus (1898)

Lopens (1923)

Boettger (1950)

Grossu (1961)

and Kisma (1965)

The variation in shell shape of British Cerastoderma edule has been noted by Boyden (1969); in fact C.edule collected from various localities around the British Isles can often be separated by their different morphological appearances. Environmental parameters, probably salinity, substratum and wave action, etc. Offect the external appearance of this cockle, resulting in various 'ecotypes', which should not however be confused whith specific differences. This plasticity in the morphology of C.edule may reflect an inherent ability to adapt within the Cerastoderma which was important in the inifial separation of these two members of the Cerastoderma.

2.) That there are only two species of the Cerastoderma:

Mars (1951)

Høpner - Petersen (1958)

Turk (1964)

Tebble (1966)

Bowden and Heppell (1968)

These three studies were concerned with the systematics of the British Lamellibranchiata (or the British Cardidae) considering again mainly shell morphology.

3.) That there are more than two species in the Cerastoderma:

Coen (1915)	-	4 species
Winkworth (1932)	-	3 species
Chavan (1945)	-	5 species

This final theory has not been supported in more recent literature. Various authorities e.g. Marx (1951) have equated the forms, regarded above as different species, into two main types; C. edule and C. glaucum. In the more recent guides to identification of marine animals (Tebble, 1966; McMillan, 1969) two species are defined - Cardium edule and Cardium lamarcki (Reeve). Haas and Knorr (1966) regard the Cerastoderma as one species - Cardium edule (L.) extending from the Mediterranean coasts to the Baltic. (Incidently, figure 490, p. 193 of Haas and Knorr is a diagram of C. glaucum, the shell exhibiting pronounced elongation of the posterior region.)

Thus the initial problem is basically, are the two Cerastoderma varieties of a single species or two distinct species, and this question has been investigated in this research.

REFERENCES

ADAMS, A. & ADAMS, H., 1958. Genera of recent Mollusca arranged according to their organisation, London, Vol. 2, pp. 454-456.

BOETTGER, C.R., 1950. Ein Beirtrage zur Frages des Ertragens von Brackwasser durch Molluskenpopulationen. Hydrobiologia, Vol. 2, pp. 360-379.

BOWDEN, J. & HEPPELL, D., 1958. Revised list of British Mollusca, part 2: Unionacea - Cardiacea. J. Conch., Vol. 26, pp. 237-272.

BOWERS, E.A., 1969. Cercaria Bucephalopsis haimeana (Lacaze-Duthiers, 1854) (Digenea: Bucephalidae) in the cockle Cardium edule L. in South Wales. J. nat. Hist., Vol. 3, pp. 409-422.

BOWERS, E.A. & JAMES, B.L., 1967. Studies on the morphology, ecology and life cycle of Meiogymnophallus minutus (Cobbold, 1859) nov. comb. (Trematoda: Gymnophallidae). Parasit. Vol. 57, pp. 281-300.

BOYDEN, C.R., 1969. Ecology of the cockle Cardium glaucum Bruguière. Essex Nat., Vol. 32, pp. 223-226.

BRACKMAN, C., 1936. Cardium edule L. var Lamarcki Reeve Basteria, Vo. 1, pp. 39-54.

BRACKMAN, C., 1937. Cardium edule L. var Clocliensis Renier. Basteria, Vol. 2, p. 25.

BRUGUIÈRE, M., 1789. Encyclopedie Methodique, Histoire Naturelle des Vers, Paris, Vol. 6, pp. 221-222.

BUCQUOY, E., DAUTZENBERG, Ph. & DOLLFUS, G., 1893. Les Mollusques marins du Roussillon, Paris, Vol. 2: Pelecypodes, pp. 251-297.

CHAVAN, A., 1945. Essai de correlation entre les varietes du Cardium edule. Bull. Mus. Hist. Nat. Paris, series 2e, Vol. 17, pp. 121-135.

CHEMNITZ, J.H., 1782. Neues Systematisches Conchylien - Cabinet Nurnberg, Vol. 6, pp. 201-202.

CHILDREN, J.G., 1823. Lamarck's Genera of Shells. Quart. Jour. Lit., Sci. and Art., Vol. 14, p. 315.

COEN, J.J., 1915. Nota sui Cardium della sezione Cerastoderma. Atti. Acc. Sci. Veneto - Trentino, serie terza, Vol. 8, pp. 54-62.

EISMA, D., 1965. Shell Characteristics of Cardium edule L. as indicators of salinity. Neth. J. of Sea Res., Vol. 2, pp. 493-540.

FISHER, P., 1887. Manuel de Conchyliologie et de Paleontologie Conchyliologique ou Histoire Naturelles des Mollusques vivant et fossiles, Paris, p. 1037.

FORBES, E. & HANLEY, S., 1853. A history of British Mollusca and their shells, London, Vol. 2, pp. 1-40.

GLEMAREC, M., 1968. Pelecypodes marins de la cote Atlantique Francaise. Publication Laboratoire de Zoologie, Brest, p. 9.

GROSSU, A.V., 1961. Variatiile lui Cardium edule L. in Marea Neagra. Hydrobiologia, Bucuresti. Vol. 3, pp. 177-191.

HAAS, W. de & KNORR, F., 1966. The Young Specialist Looks at Marine Life. Burke, London, pp. 192-193.

HANCOCK, D.A., 1967. Growth and mesh selection in the edible cockle (Cardium edule L.). J. appl. Ecol. Vol. 4, pp. 137-157.

HANCOCK, D.A. & URQUHART, A.E., 1965. The determination of natural mortality and its causes in an exploited population of cockles. (Cardium edule L.). Fishery Invest. Lond., ser. 2, Vol. 24 (2) pp. 1-23.

HANLEY, S., 1856. Recent shells, London, pp. 134 and 365.

HØPNER-PETERSEN, G., 1958. Notes on the growth and biology of the different Cardium species in the Danish brackish water areas. Medd. Dan. Fisk-og Havunders. Nyserie, Vol. 2, no. 22, pp. 1-31

HØPNER-PETERSEN, G., 1968. Marine Lamellibranchiata. Zoology of the Faroes Copenhagen, pp. 53 and 57.

JAMES, B.L. & BOWERS, E.A., 1967. The effects of parasitism by the daughter sporocysts of Cercaria Bucephalopsis haimeana (Lacaze-Duthiers, 1854) on the digestive tubules of the cockle Cardium edule L. Parasit., Vol. 57, pp. 67-77.

KALTENBACH, H., 1943. Die Cardienfauna der beiden Brackwasserseen von El Caefia bei Bengasi. Arch. Molluskenk, Vol. 75, pp. 132-145.

LINNEUS, C.V., 1758. Systema Naturae, edit. 10. Vol. 1, p. 681.

LOPPENS, K., 1923. La variabilite chez Cardium edule. Ann. Zoo. Soc. Belg., Vol. 54, pp. 33-67.

MARS, P., 1951. Essai d'interpretation des formes generalement groupees sous le nom de Cardium edule L. Bull. Mus. Hist. Nat. Marseilles, Vol. 11, pp. 1-31.

MARTEN, E.V., 1870. Zoological literature on the Mollusca. Zool. Rec., Vol. 6, pp. 586-587.

McMILLAN, N.F., 1968. British shells (wayside and Woodland Series), p. 88. Warne, London.

MOORE, R.C., 1969. Ed. Treatise on Invertebrate Palaeontology. Mollusca 6. Bivalvia Part N, Vol. 2, (of 3), pp.N 583- 590. Geol. Soc. of Amer. Inc. & Univ. of Kansas.

MORCH, O.A.L., 1853. Catalogus Conchyliorum de Yoldi, Vol. 2; p. 34.

MORTON, B.S., 1970. The tidal rhythm and rhythm of feeding and digestion in Cardium edule. J. mar. biol. Ass. U.K., Vol. 50, pp. 499-512.

MUUS, B.J., 1967. The fauna of Danish estuaries and lagoons; distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. Medd. Dan. Fisk - og Havunders. Ny serie, Vol. 5, pp. 157-162.

MUUS, B.J., 1968. Some problems facing the Ecologist concerning races and sub-species of brackish water animals, (in Estuaries, ed. G.H. Lauff), pp. 558-563. Washington (D.C.) Amer. Assoc. for the Adv. of Sci.

NEWELL, R.C. & NORTHCROFT, H.R., 1967A reinterpretation of the effect of temperature on the metabolism of certain marine invertebrates. J. Zool. Lond. Vol. 15, pp. 277-298.

OPINION, 184, 1954. Opinions and declarations rendered by the International Commission on Zoological Nomenclature, London, Vol. 3 pp. 27-35.

OPINION, 427, 1956. Opinions and declarations rendered by the International Commission on Zoological Nomenclature, London, Vol. 14, pp. 281-310.

PALLARY, P., 1919. Etudes de Malacologie retrospective, I. Poiret. J. Conchyl (Paris), Vol. 64, pp. 12-13.

POIRET, I., 1789. Voyage en Barbarie ou lettres ecrites de Numidie, Paris, Vol. 2, p. 13.

POLI, I.X., 1795. Testacae Utrisque Sicieiae corumque Historia et Anatome, Vol. 2, p. 258.

REEVE, L.A., 1845. Monograph of the genus Cardium. Conchologifa Iconica, Vol. 2 (1843), species number 93.

RENIER, S.A., 1804. Tavola Alfabetica delle Conchiglie Adriatiche, Padova, Species number 65, p. 6.

ROMER, E., 1869. Die familie der Herzmuscheln, Cardiacea System. Conchilien-Cabinet von Martini and Chemnitz, Ed. Kuster, section 57, p. 124.

RUSSELL, P.J.C., 1969. Studies on the ecology, distribution and morphology of the cockles Cardium edule L. and C. glaucum (Bruguière). Ph.D. Thesis, London.

SHERBORN, C.D., 1902. Index Animalium 1758-1800, p. 425.

TEBBLE, N., 1966. British Bivalve Seashells, pp. 95-108. Trustees of the British Museum (Natural History), London.

TURK, S.M., 1964. The British species of Cardium. The Conchologists Newsletter, Conchological Society of Great Britain and Northern Ireland, no. 10, pp. 58-62.

WINCKWORTH, R., 1932. The British Marine Mollusca. J. Conch, Vol. 19, pp. 211-252.

SECTION - 11

SECTION II

USE OF MORPHOLOGICAL SHELL CHARACTERISTICS TO SEPARATE THE BRITISH CERASTODERMA.

The fact that the Danish Cerastoderma could be divided into two distinct types: C. edule and C. lamarcki (= glaucum) was first realised by Høpner-Petersen (1958). He formulated the following diagnostic characteristics for the separation of the two cockles:

Shell character		C. edule	C. glaucum
Ribbing	-	Middle part of shell flat, ribs with small, widely spaced scales.	Ribs sharp, with small triangular scales close together, composed of periostracum.
Ribs on posterior part of shell.	-	Well developed.	Poorly developed.
Posterior valve junction	-	Crenulate	Almost linear
Periostracum	-	Poorly developed.	Thick, covers about 75% of shell surface.

To this list can be added the fact that the hinge ligament is short and confined to within the umbo in C. glaucum, whereas in C. edule it is long and unrestricted. This latter character-istic plotted against shell breadth (- width across the shell valves) to produce a bivariate scatter pattern, was used by Høpner-Petersen to discriminate graphically between the two Cerastoderma. Taking the x - axis as breadth of shell and the y - axis as ligament length, he separated the two cockle types by the linear function $x = 3.5y + 2$, all those above the line (i.e. with a long ligament) being C. edule, and all those below the line (i.e. with a short ligament) being C. glaucum.

In general, C. edule is more or less oval, tending towards anterior-posterior symmetry, whilst C. glaucum is elongated posteriorly (see plate 1). The posterior region of the shell of this latter cockle is often angled or wedge shaped (giving an interrupted shell outline at the transition from the smooth curve of the middle shell to the posterior elongation) whereas in C. edule the shell valves are more completely smoothly rounded. In large, older individuals of C. edule there is also a tendency for the valves to elongate posteriorly, but these specimens can easily be separated from C. glaucum by the fact that the ligament is also correspondingly longer.

Tebble (1966) considered that the extent to which the marginal crenulations on the inside of the shell valves extended towards the umbo, was also of value in discriminating between the two Cerastoderma. Thus he records these crenulations as only occurring at the margins in C. edule, whereas in C. glaucum they continue as furrows towards the umbo. However Turk (1964) records the internal shells of both cockles as being fluted only at the margins. Russell (1969) studied this characteristic and concluded that the young individuals of both C. edule and C. glaucum are ribbed internally. The apparent internal ribbing of C. glaucum reflects the external shell ribbing, being visible in lagoon C. glaucum because the shell is thin. In addition, Russell also noted that the pointed ribs of C. glaucum, in contrast to C. edule, are due, not only to the triangular shaped scales of the periostracum covering the ribs, but also to the shape of the calcified part of the ribs themselves, which are sharply pointed.

As Russell has thoroughly studied these characteristics only a few additional observations are included here.

In a comprehensive study of the characters above, Russell (1969) concluded that several of the morphological features, including the form of the ribs, the cover of periostracum and the shape of the posterior

shell margin, must be taken into account to effectively separate the two cockles, especially from mixed populations. The value of some of the discriminating characteristics of earlier workers, when applied to the British Cerastoderma, is considered in this section.

1. Relationship of ligament length to shell breadth in various cockle populations.

(a) Arithmetric plots

The above relationship was used by Høpner-Petersen (1958) to separate the two Cerastoderma in mixed Danish populations. His discriminating function $x = 3.5y + 2$ has been applied to British and Danish single and mixed cockle populations by Russell (1969) who calculated the four functions which best fit* C. edule and C. glaucum from separate and mixed cockle populations. These were:-

$y = 0.475x - 2.616$ - C. edule from separate populations

$y = 0.235x - 0.610$ - C. glaucum " " "

$y = 0.427x - 1.177$ - C. edule from mixed populations

$y = 0.306x - 1.361$ - C. glaucum " " "

Application to cockle populations from South-East England

The following procedure was used in the study described here. The ligament length and shell breadth of cockles was measured by vernier calipers to the nearest 0.05mm. Because Høpner-Petersen found that the function $x = 3.5y + 2$ only applied to cockles of shell breadth greater than 5mm., which excludes recently settled juveniles, in this study only animals greater than 7.9mm. shell breadth were considered.

* In a graphical treatment of functions defining the two cockles, the lines describing the functions are, for the purposes of this study, called the lines of fit.

Cockle populations from the following localities were investigated:-

i) C. edule: separate populations from Southend, Essex, and Whitstable, Kent.

ii) C. glaucum: separate populations from New England Creek, Essex,
Widewater, Sussex,
Cuckmere Haven, Sussex,
and Horsey Island Lake, Hampshire.

and iii) Mixed Cerastoderma populations from the estuaries of the River Crouch and Roach, Essex.

The relationships obtained between ligament length and shell breadth for these various Cerastoderma populations are shown in figures 1 - 3. It can be seen from fig. 1 a, b, c, d, that in general the majority of C. glaucum individuals are found beneath the discriminating line of $x = 3.5y + 2$ of Høpner-Petersen, but that in two of the cockle populations, from Widewater and Cuckmere Haven, a high proportion of individuals are found above the line, and would thus be wrongly classified as C. edule. Within the range of shell breadth from 7 - 25mm. the line of fit for the function $y = 0.235x - 0.610$ calculated by Russell for separate C. glaucum populations is good for the measurements obtained from the New England Creek, Essex cockles. As he did not study this population it would seem that his line is successful in indicating a homogeneous C. glaucum population. However, in the other populations from Widewater, Cuckmere Haven and Horsey Island Lake, his line of fit is not always good even though he sampled these populations to obtain his mean function.

The majority of C. edule from the populations examined, fall above the Høpner-Petersen discriminating function, see figures 2a and b, and therefore this line is of value in indicating homogeneous populations of this cockle. Likewise the best fit lines of Russell (1969) for C. edule from single cockle populations agree tolerably well with the data graphed in figures 2a and b.

Fig - 1

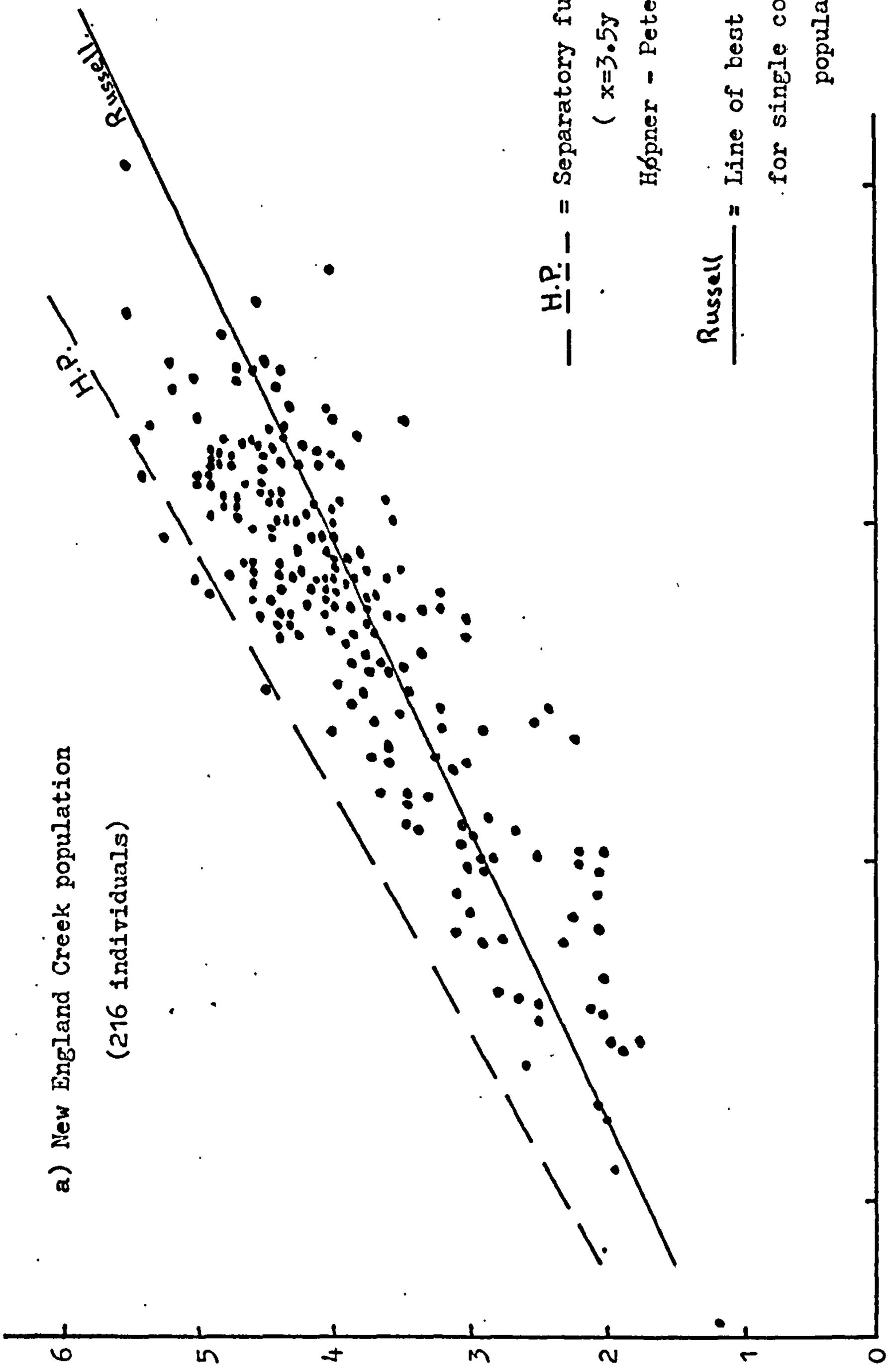
Relationship of ligament length to shell breadth in various lagoon populations of Cerastoderma glaucum:

a) New England Creek, Essex

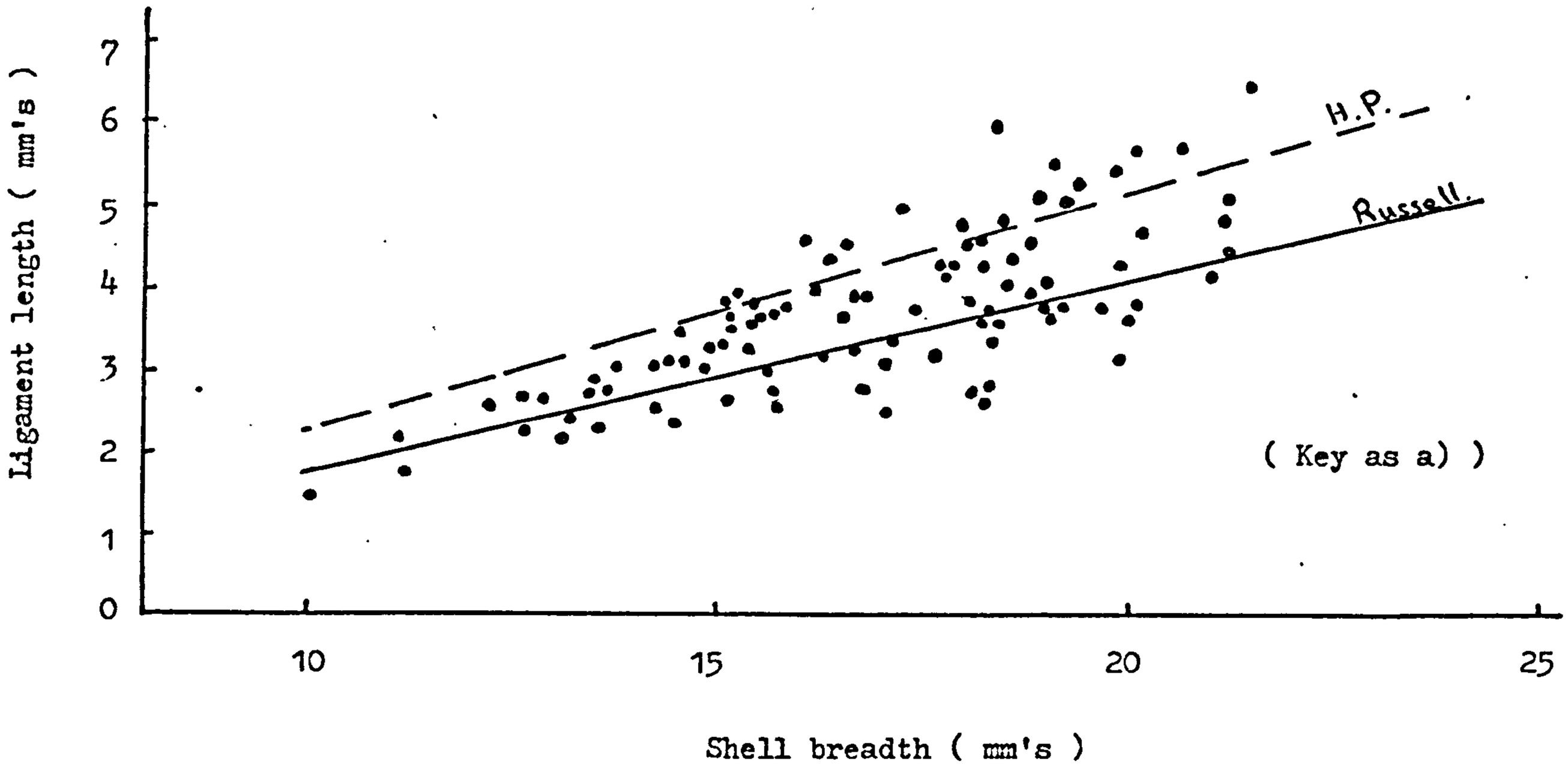
b) Widewater, Sussex

c) Cuckmere Haven, Sussex

d) Horsey Island Lake, Hampshire


a) New England Creek population
(216 individuals)
H.P.
Russell
Shell breadth (mm's)
Ligament length (mm's)
0
1
2
3
4
5
6
10
15
20
25
H.P. = Separatory function
(x=3.5y + 2) of
Hôpner - Petersen
Russell = Line of best fit of Russell
for single cockle C.glaucum
populations

b) Widewater population
(100 individuals)



c) Cuckmere Haven population
(120 individuals)

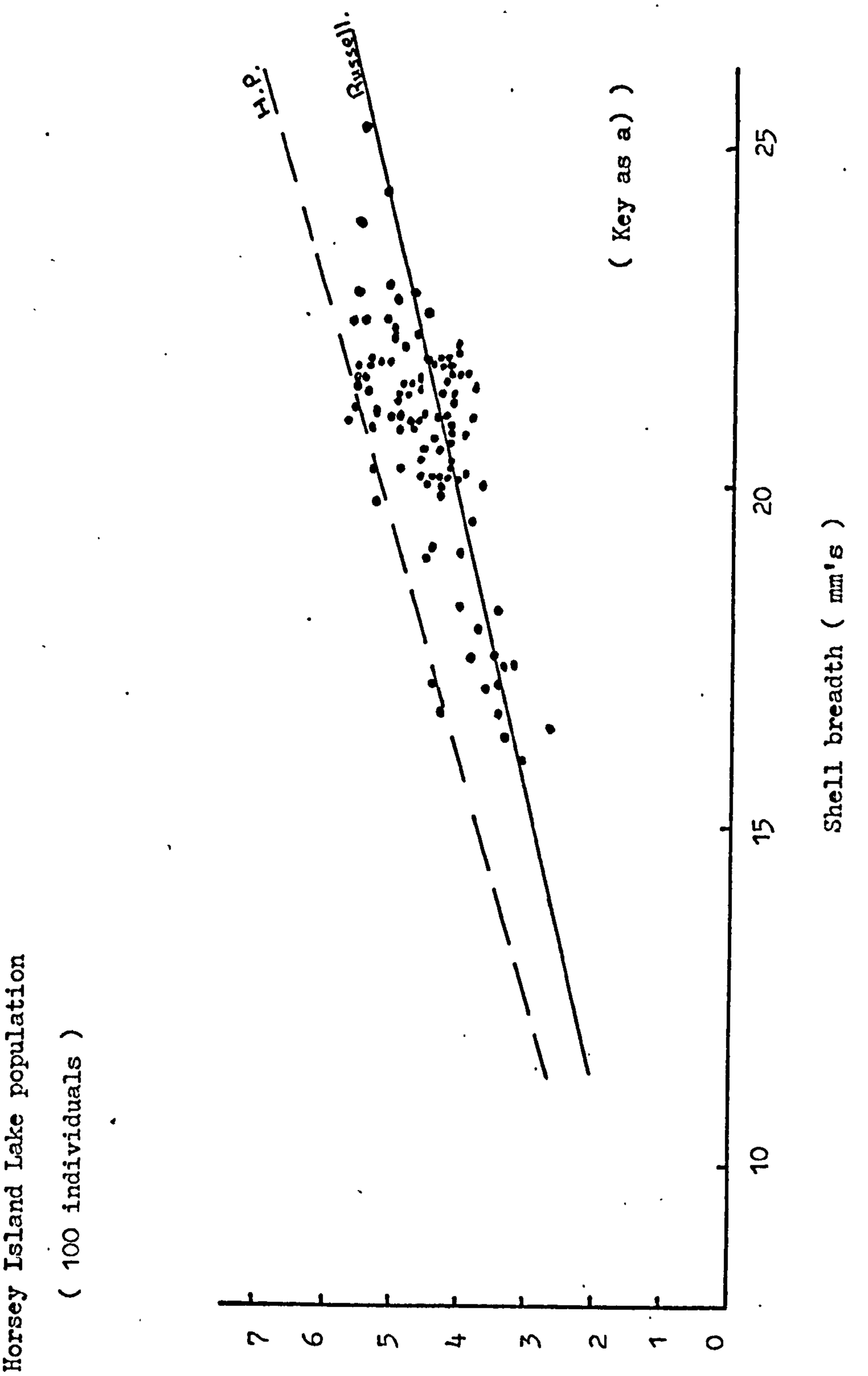
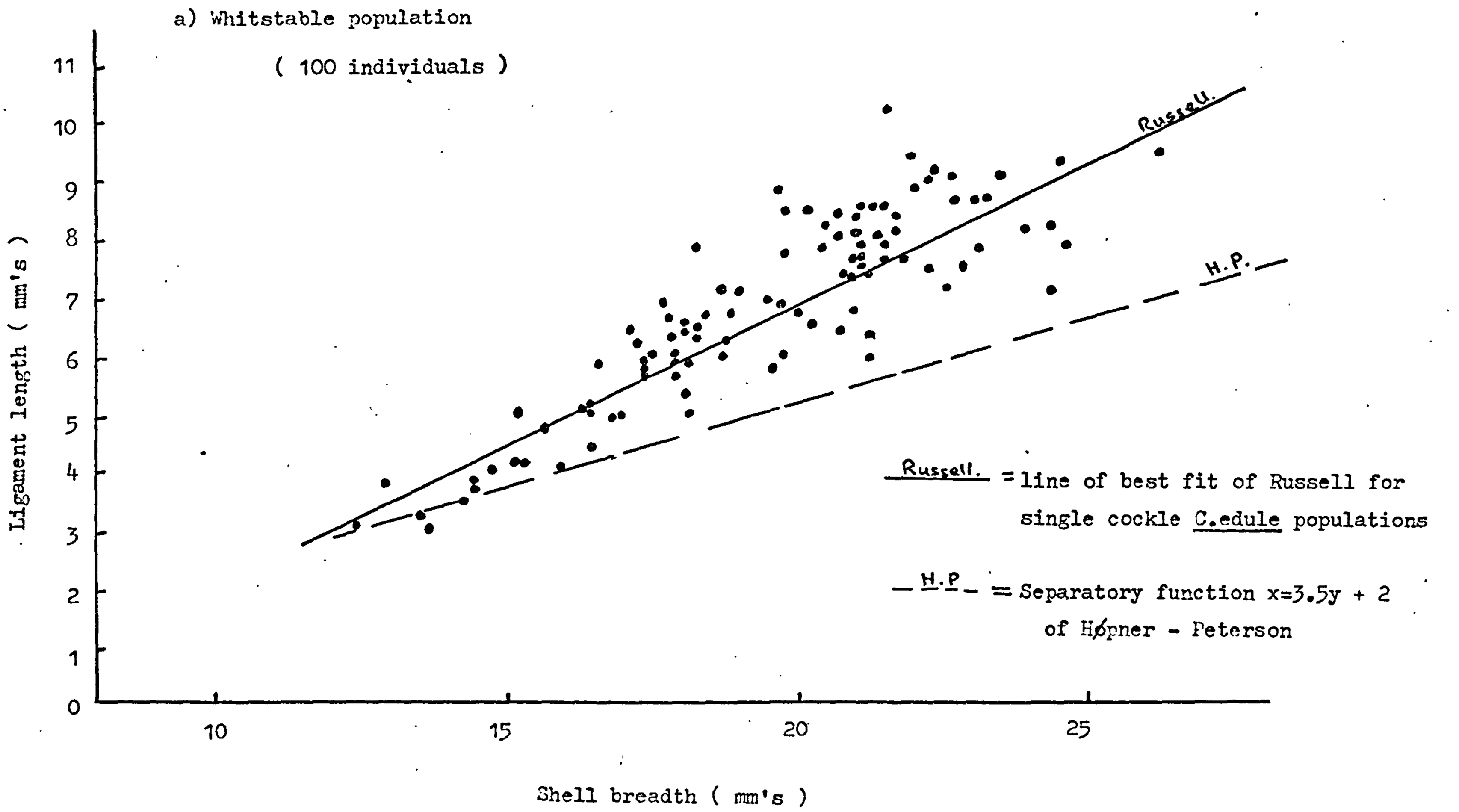

H.P.
Russell.
(Key as a))
25
20
15
10
Shell breadth (mm's)
d). Horsey Island Lake population
(100 individuals)
Lligament length (mm's)
0 1 2 3 4 5 6 7

Fig 2 - Relationship of ligament length to shell breadth in littoral populations of C.edule



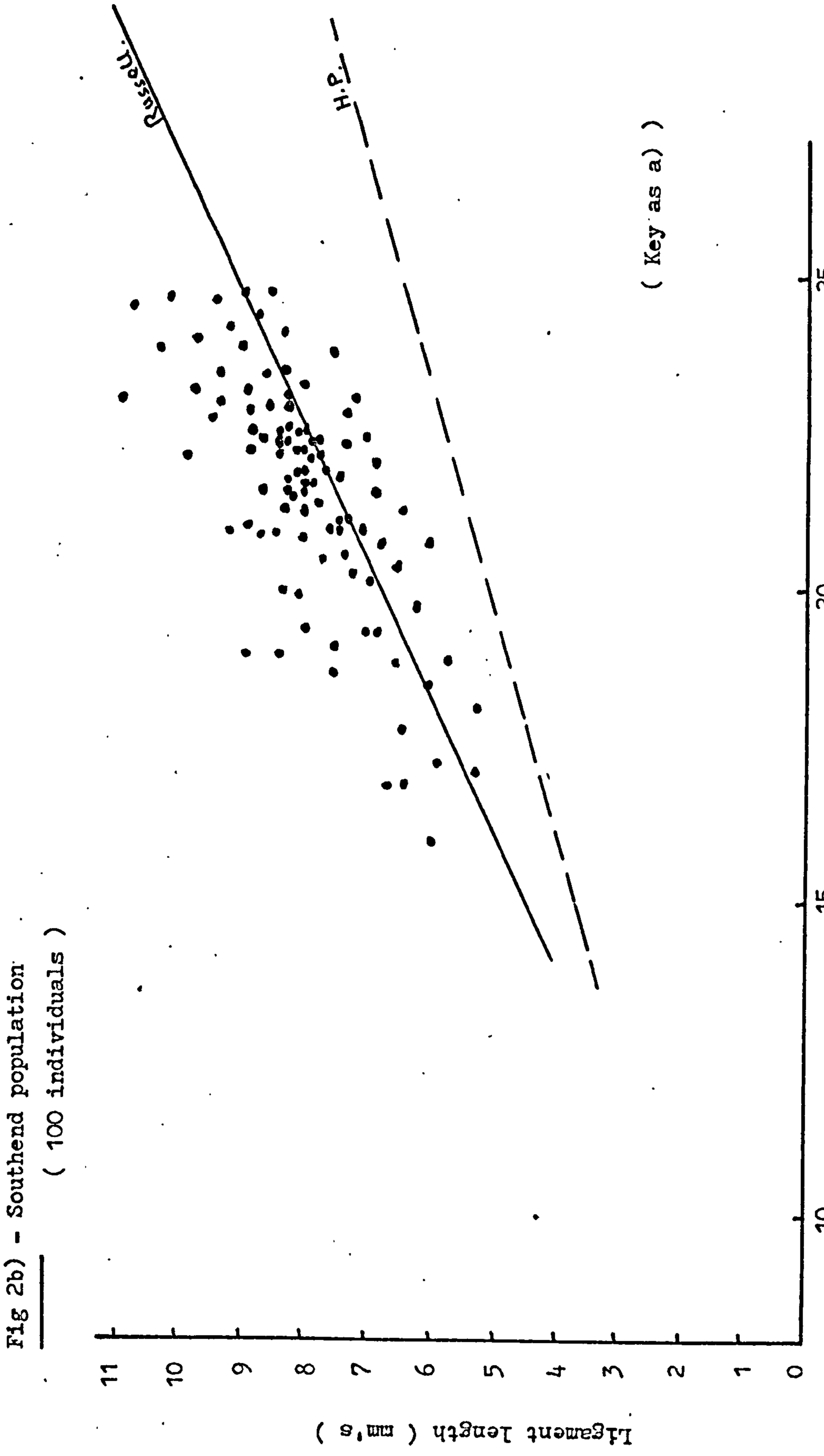


Fig 2b) - Southend population
(100 individuals)

The two Cerastoderma from the Crouch and Roach mixed cockle populations were separated using the shell characteristics noted earlier. The ligament lengths/shell breadths were graphed as above for the two cockles, and the result is shown in fig. 3a & b. In these mixed populations the cockles are large up to 35mm. broad, compared with a maximum of 24mm. used by Høpner-Petersen. It is obvious here that in large cockles the discriminating function of Høpner-Petersen is of no practical value, and clearly the ratio of ligament length to shell breadth is an example of allometry. The best lines of fit of Russell (1969), for single and mixed cockle populations, can also be criticised from a similar stand point, and as can be seen in figs. 3, they are also of little value in separating the two forms from mixed populations.

Thus in cockles, between 7 - 24mm. shell breadth, from single cockle populations, the discriminating function of Høpner-Petersen (1958) and more particularly the lines of fit of Russell (1969), are of value in indicating the cockle type. However, in mixed populations where large cockles are found the discriminating function is unsuccessful in separating the two cockles. Although the best line of fit of Russell for C. edule from mixed Cerastoderma populations approximates to the distribution of ligament length/breadth found in C. edule from the Crouch and Roach, the line for C. glaucum is less good. It would seem that if there is a relatively large number of points below Høpner-Petersen's discriminating line, then this indicates the presence of C. glaucum in the cockle population.

(b) Logarithmic plotting of ligament length/shell breadth data.

Pholo (1963) pointed out that the relationship between ligament length and shell breadth was an example of allometric growth, so that with increasing size, ligament length/shell breadth increases differentially. For this reason he argued that an arithmetric plot of the two variables

Fig 3 - Relationship of ligament length to shell breadth in C.edule from mixed cockle populations.

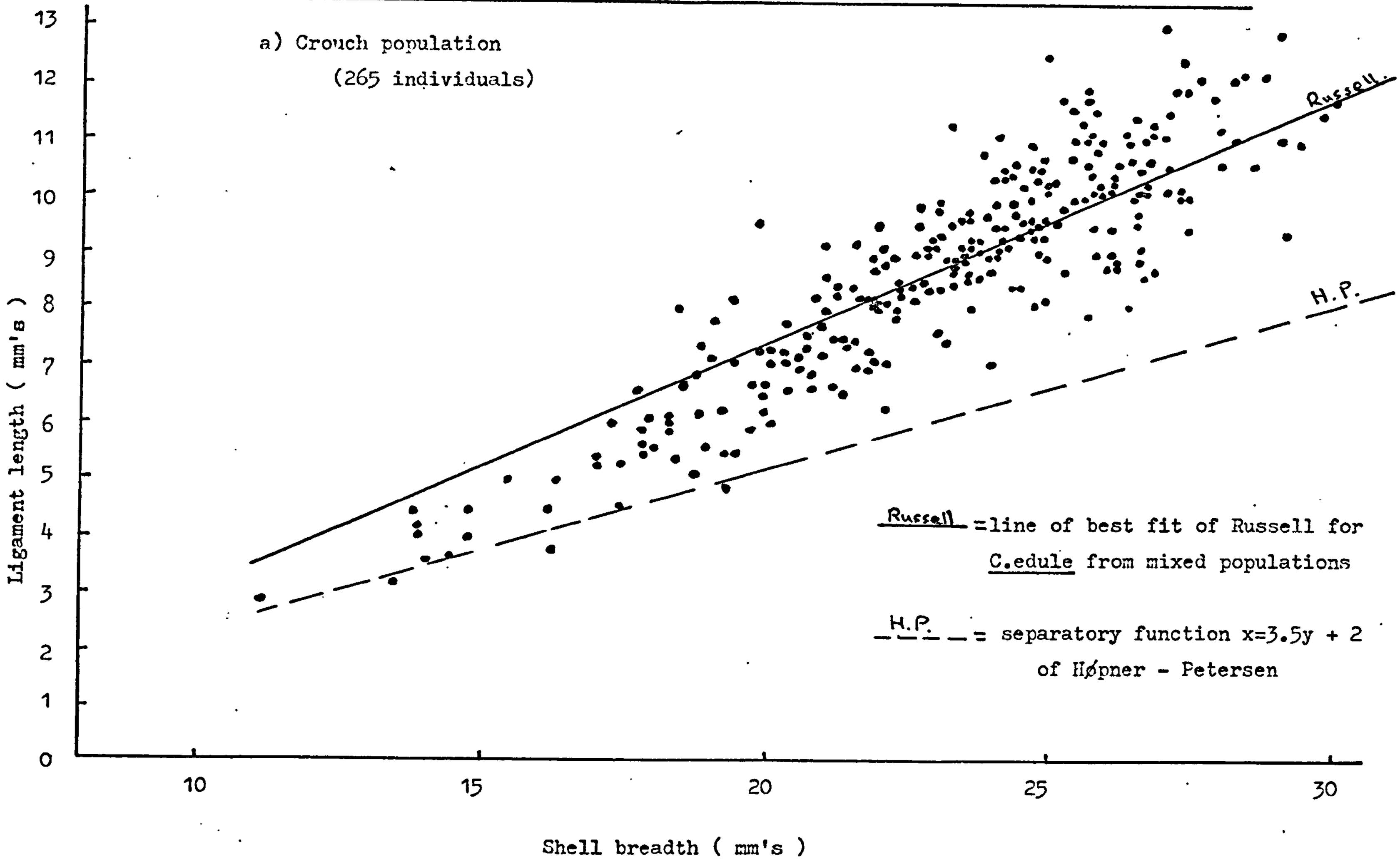


Fig 3b) - Roach estuary population

(210 individuals)

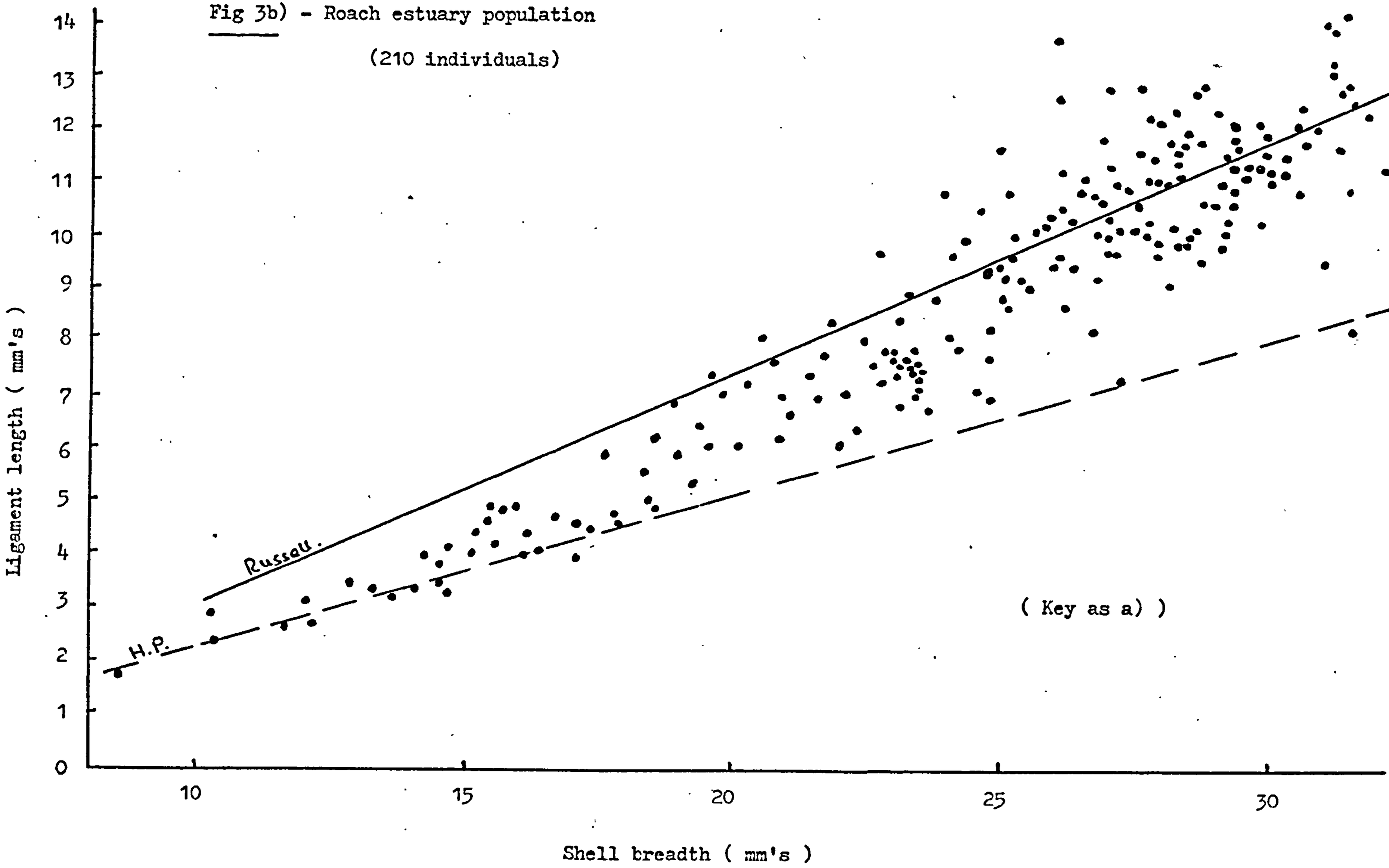


Fig 3c/d Relationship of ligament length to shell breadth in the two Cerastoderma from mixed populations.

c) Crouch population.

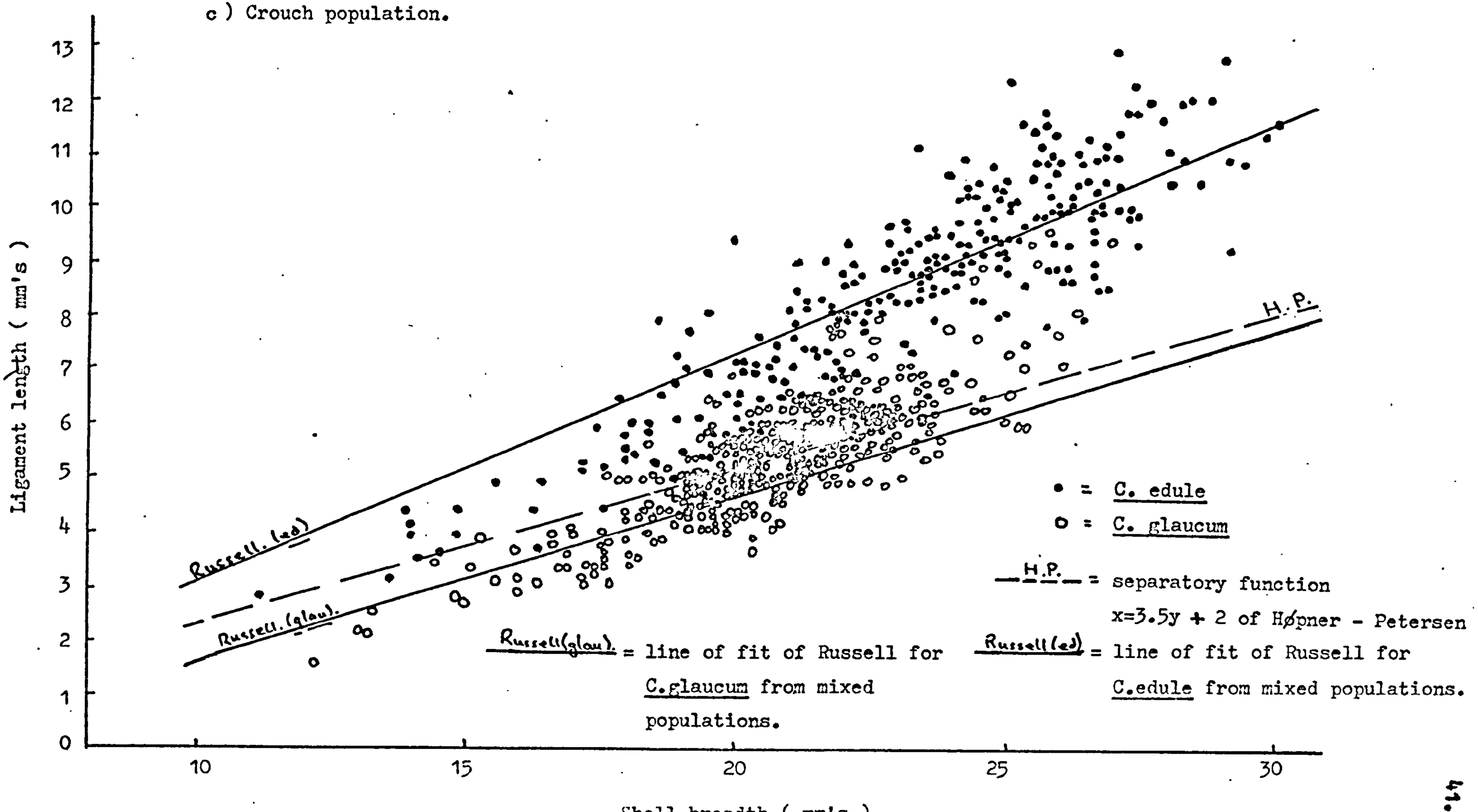
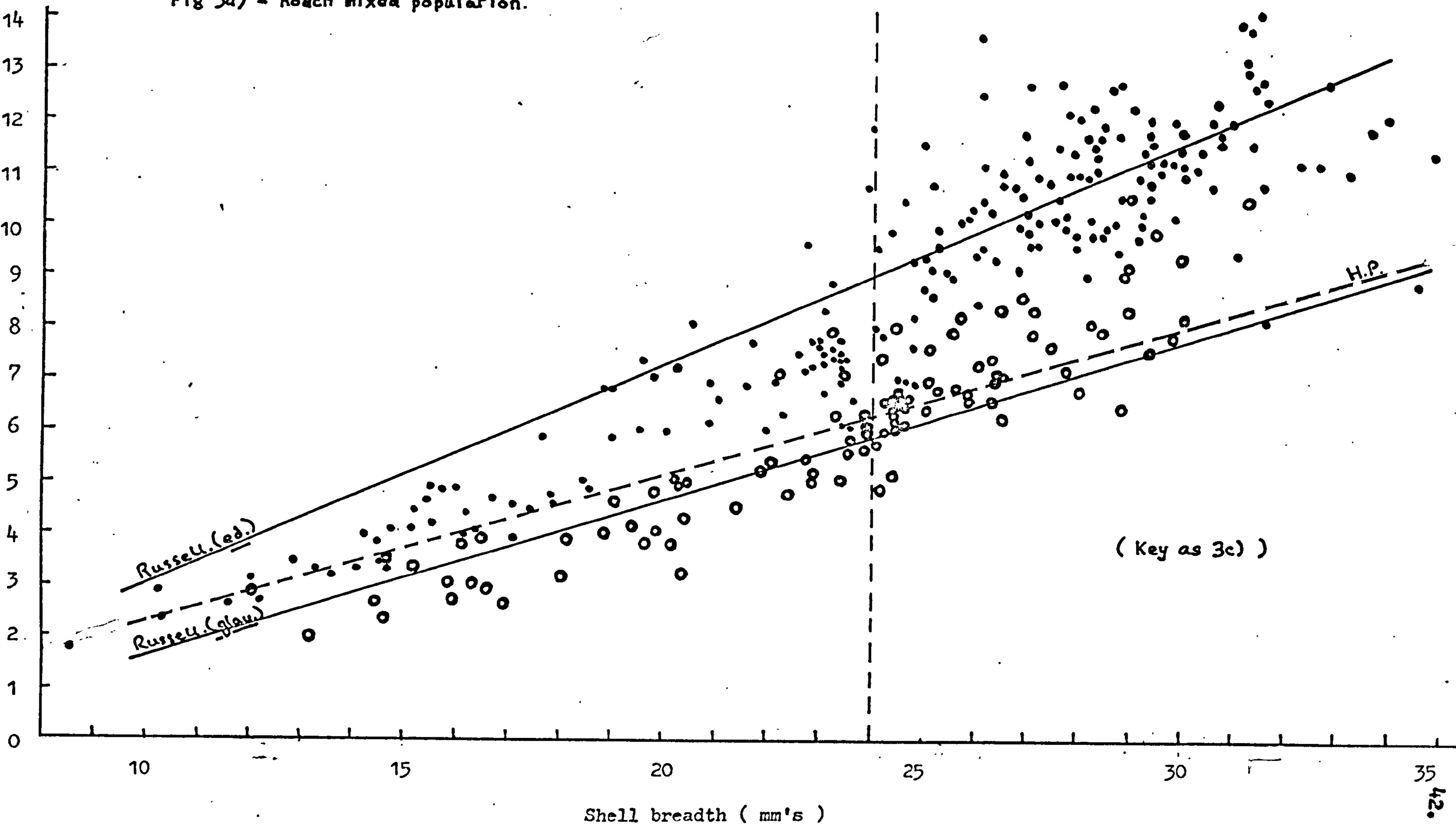


Fig 3d) - Roach mixed population.



could not give a linear function that would separate the two cockles.

To overcome this problem, Pholo (1963) modified the treatment of the ligament length/shell breadth data, by converting it to a double logarithmic plot, so that a linear discriminating function could then be employed.

The discriminating function determined by Pholo is as follows:-

$y = 0.395910$ (log. breadth) + (-0.385956)(log. lig. length)

where if $y < 0.259920$ the individual is C. edule

and if $y > 0.259920$ " " " C. glaucum.

This function was produced considering a mixed Cerastoderma population from Gullmars Fjord, Sweden. The sample used by Pholo to obtain this discriminating function, was however small in size (100 cockles) and the maximum ligament length about 6.5mm's, indicated that he was considering only a small range of size groups. The error in this population, both calculated and practically determined by Pholo, was in the order of 10%.

In contrast to these cockles, the maximum ligament length of the English Cerastoderma from the Roach and Crouch mixed populations was in the region of 13mm's, double the size of those used by Pholo.

The double logarithmic transformation of the measurements of ligament length to shell breadth for various Cerastoderma populations from south-east England are shown in figures 4 - 6.

C. edule, from a single cockle population at Whitstable, Kent, fig. 5 and from the mixed Cerastoderma populations of the Roach and Crouch, fig. 6 are always to one side of Pholo's linear discriminating function. Thus this function is of use in identifying cockle populations. It would seem that if an individual from 15 - 30mm. shell breadth falls below this line, then the cockle is C. glaucum.

However single cockle C. glaucum populations, see fig. 4, do not fall to one side of the discriminating function of Pholo. It can also

Fig 4 - Relationship of log. ligament length to log. shell breadth in various lagoon populations of C. glaucum.

a) Cuckmere Haven population

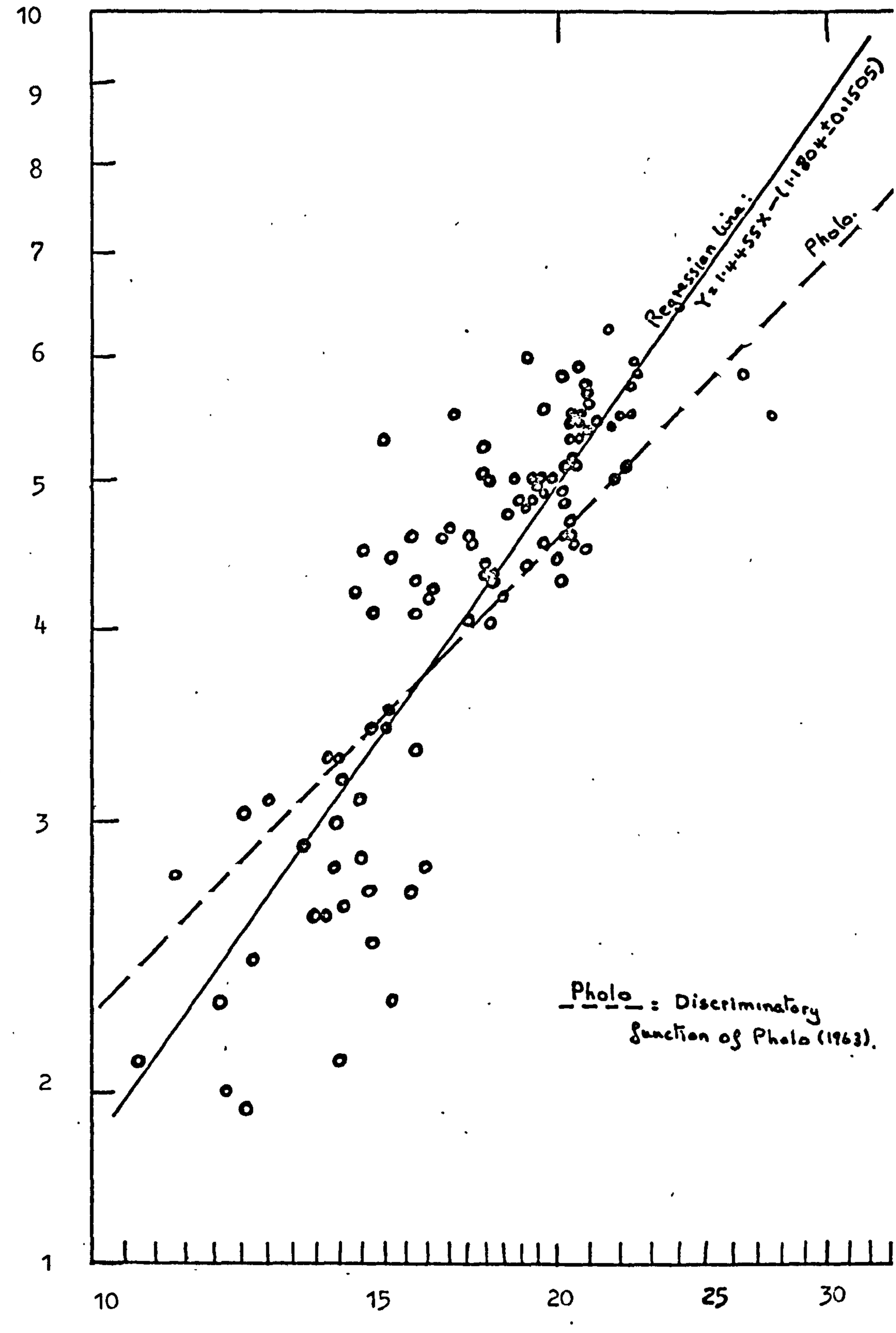


Fig 4b) - New England Creek C.glaucum population.

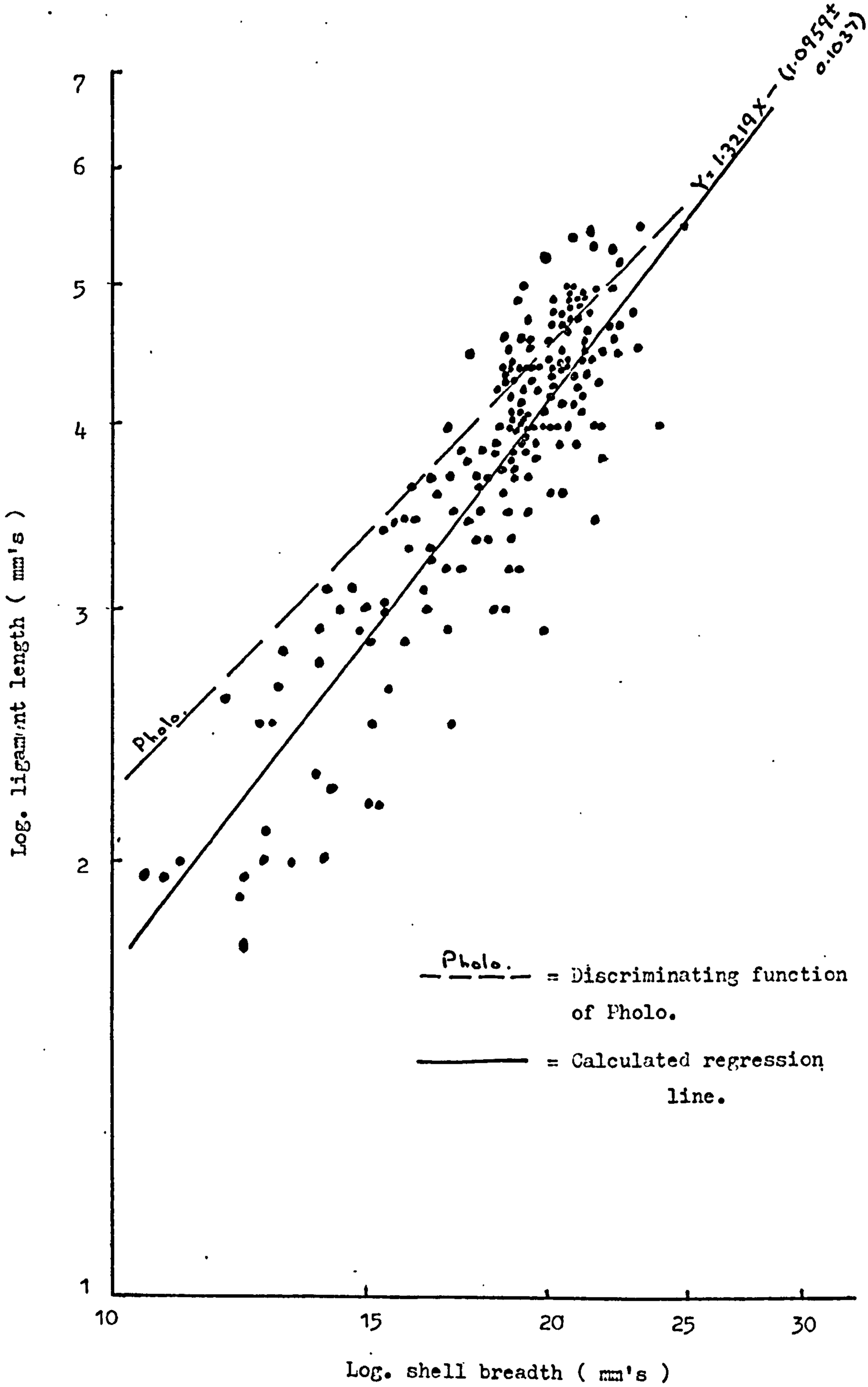
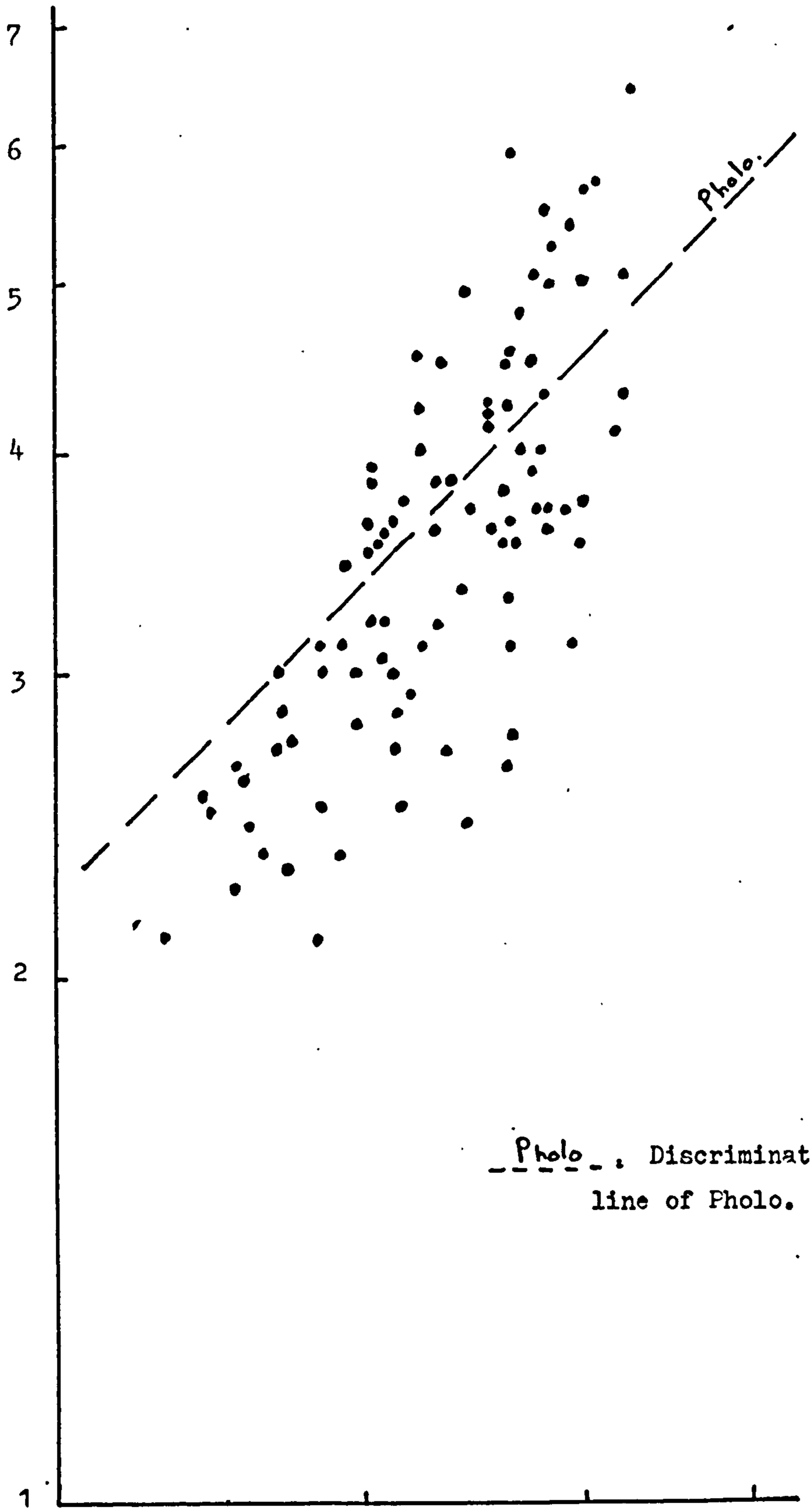
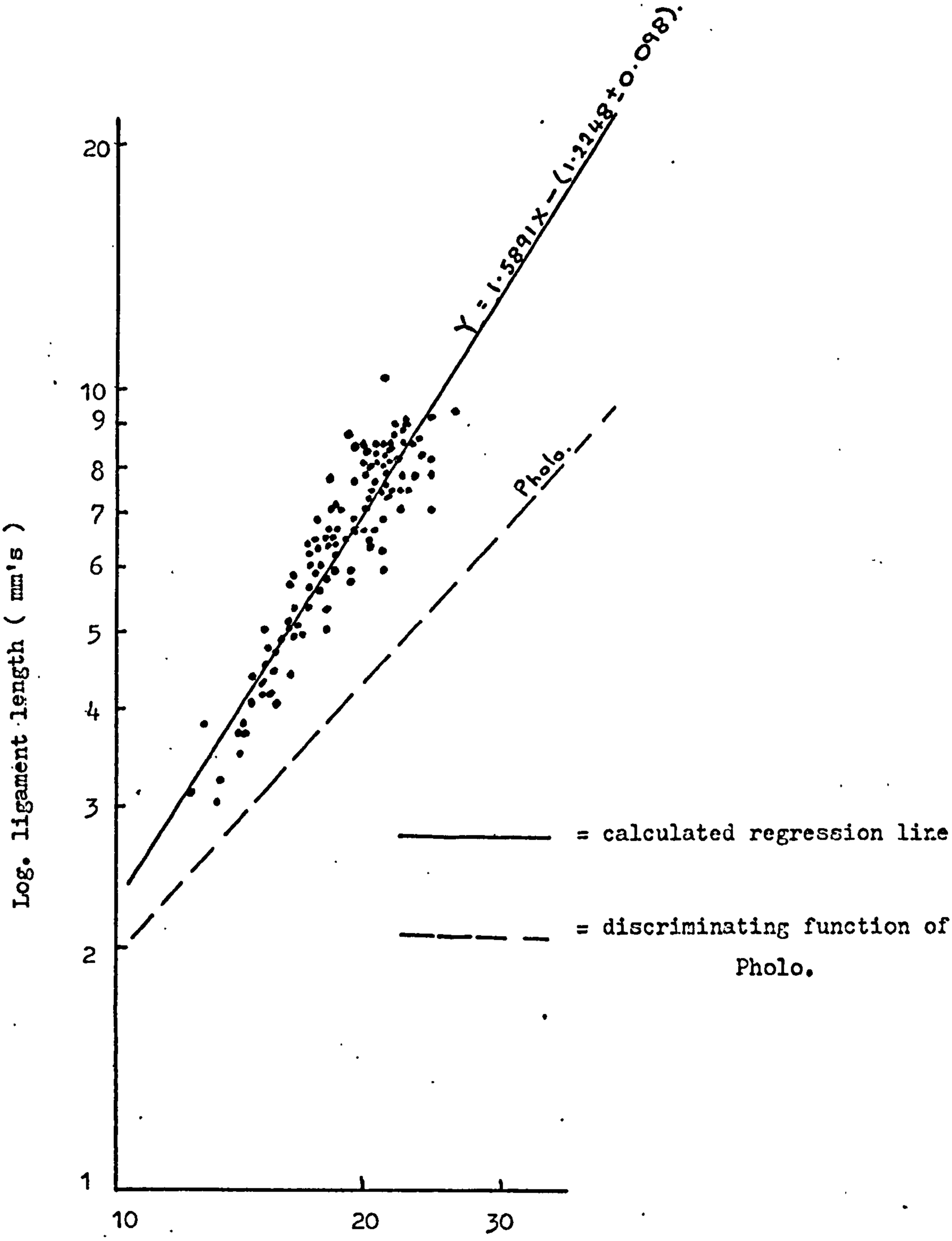


Fig 4c) - Widewater C. glaucum population



Pholo. Discriminating line of Pholo.

Fig 5- Relationship of log. ligament length to log. shell breadth in a single cockle, C. edule, population from Whitstable, Kent. The calculated regression line and discriminating function of Pholo (1963) have also been included.



be clearly seen in the graphs of ligament length to shell breadth of cockles from the Roach and Crouch estuaries shown in fig. 6 that the discriminating function of Pholo does not separate C. edule from C. glaucum in individuals larger than 15mm. shell breadth.

An alternative approach to this problem is to calculate the 95% confidence limits around the regression function for both cockles from a mixed population. Unfortunately, in measurements from cockles originating from a mixed population, (see fig. 7), an overlap in the confidence limits occurs particularly amongst the larger size groups. Therefore, considering the logarithmic data, no rigid rules can be concluded as regards to the separation between the two forms in mixed populations.

The calculated regression functions (for method, see Appendix VI) for various Cerastoderma populations can be found in table 1. The lines for these populations have been superimposed on the distribution patterns of log. ligament length to log. shell breadth in figures 4 - 6. These regression lines, with 95% confidence limits, for C. edule and C. glaucum from separate cockle populations are shown in fig. 8.

Considering cockles greater than 12mm. shell breadth, because the upper line of the 95% confidence limit of C. glaucum does not cross the regression line for C. edule, where they have been calculated from separate cockle populations, it can be concluded, that in a sample of cockles:-

(1) if individuals are found above the regression line for C. edule and below the regression line for C. glaucum, then a mixed population is indicated.

(2) if individuals are found above the regression line for C. edule, then they are certainly C. edule.

(3) if individuals occur below the regression line for C. glaucum, they are certainly C. glaucum.

Fig 6a) - Relationship of log. ligament length to log. shell breadth in cockles collected from the Crouch mixed population.

The distribution of C.edule, calculated regression lines for C.edule and C. glaucum and the discriminating function of Pholo (1963) are also included.

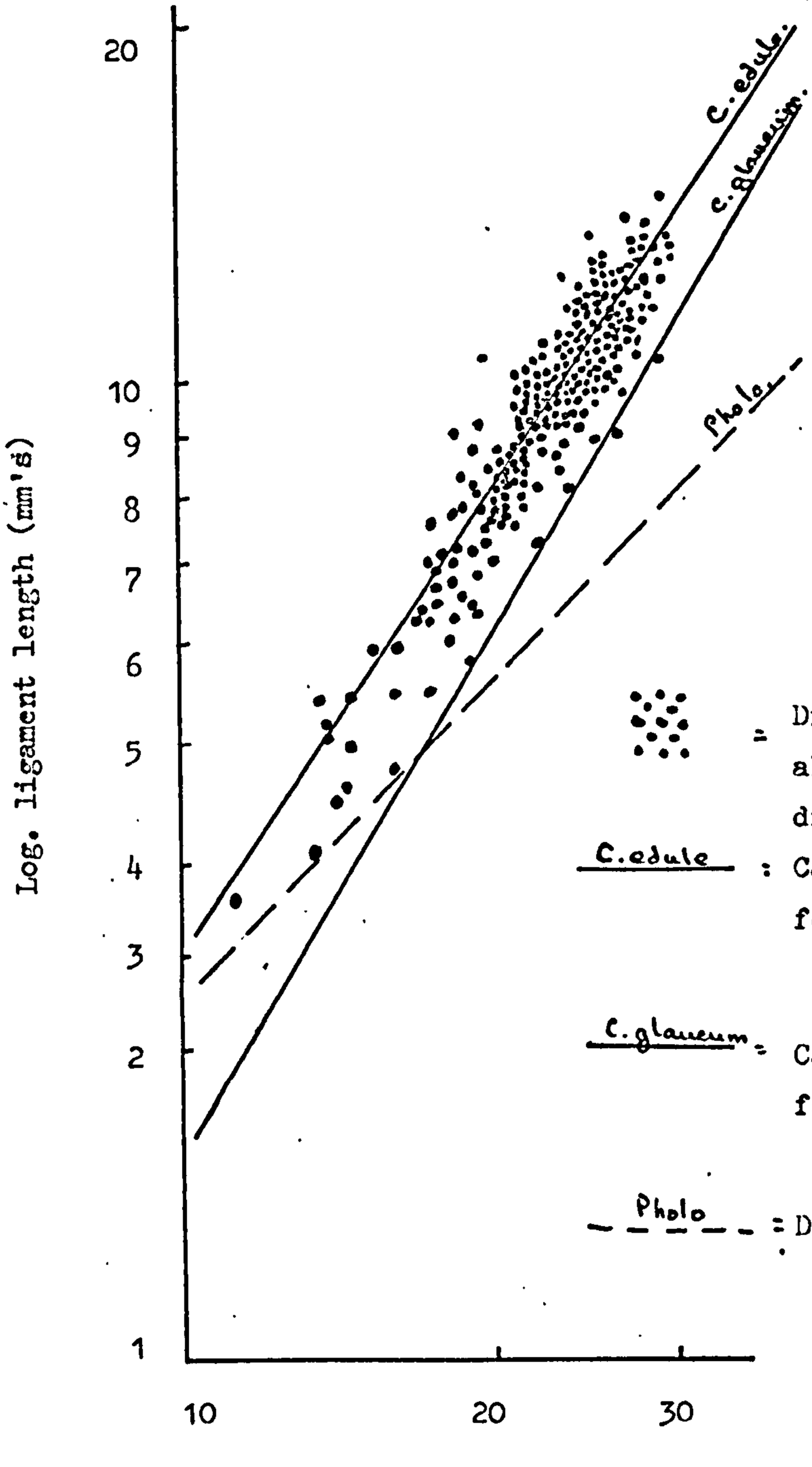


Fig 6b) - Relationship of log. ligament length to log. shell breadth in cockles collected from the Roach mixed population.

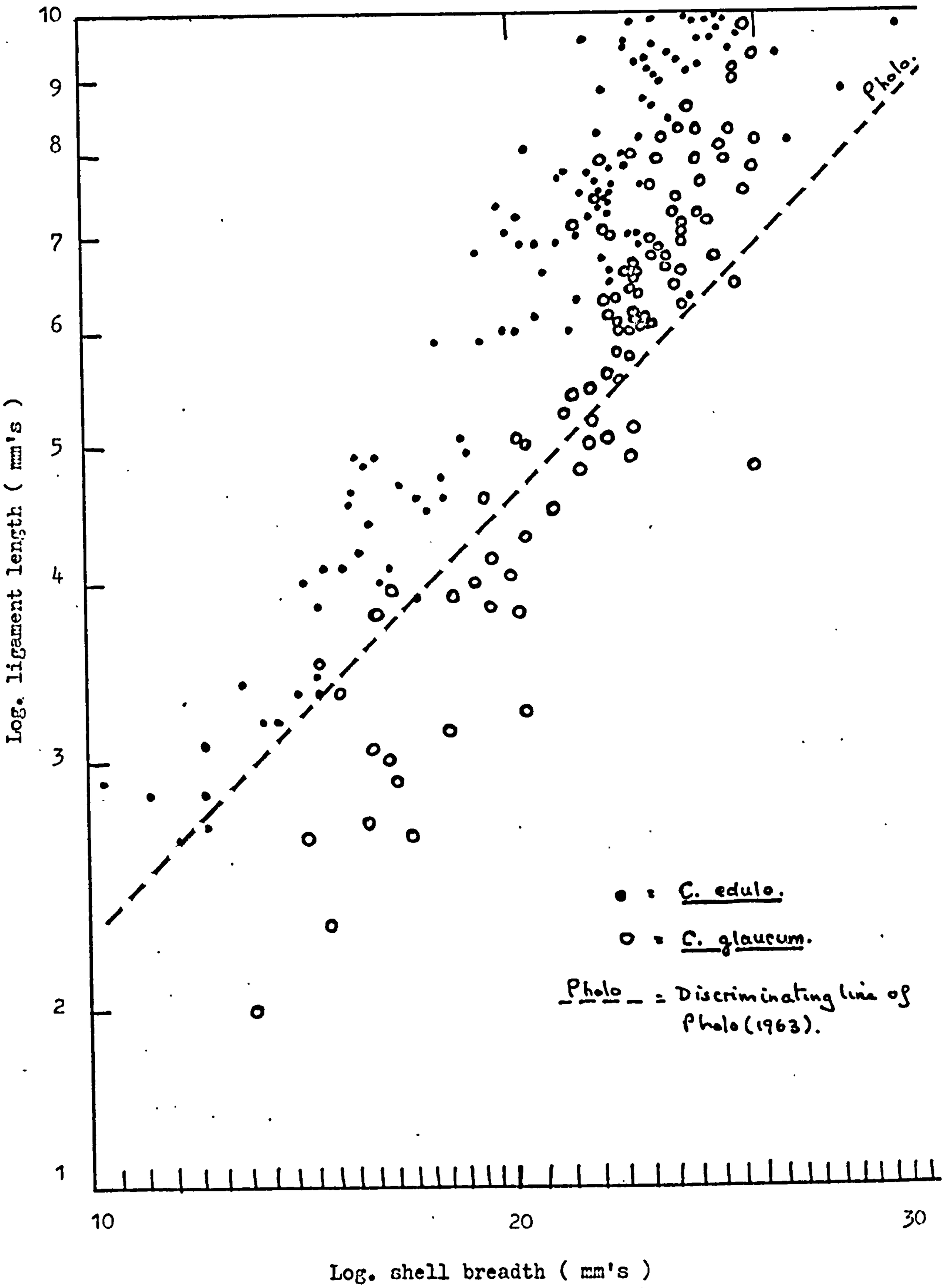


Table 1

Statistical analysis of the log. ligament length / log. shell breadth data for various cockle populations from south - east England.

Locality of *C.edule* Whether from a separate or mixed population.	Number in sample - (n)	Calculated regression line + 95% confidence limits.	Correlation coefficient - (r)
* Whitstable, Kent - separate	101	$y = 1.5891x - (1.2248 \pm 0.098)$	0.9063
Crouch estuary, Essex - mixed	170	$y = 1.5189x - (1.1322 \pm 0.2334)$	0.6413
Locality of *C.glaucum*			
Widewater, Sussex - separate	96	$y = 1.3538x - (1.1659 \pm 0.2017)$	0.7978
Cuckmere Haven, Sussex - "	71	$y = 1.4455x - (1.1804 \pm 0.1505)$	0.8424
Horsey Island Lake, Hants. - "	100	$y = 1.1390x - (0.8483 \pm 0.0876)$	0.6962
New England Creek, Essex - "	200	$y = 1.3219x - (1.0959 \pm 0.1037)$	0.8768
* Total *C.glaucum* from separate pops.	467	$y = 1.2510x - (0.9889 \pm 0.1270)$	0.8316
Crouch estuary, Essex - mixed	170	$y = 1.6843x - (1.4828 \pm 0.1805)$	0.6558

Where y = log. ligament length & x = log. shell breadth.

(All the correlation coefficients above are significant at the 0.001% level.)

* - The t-test comparing the slopes of the regression lines for separate populations of *C.edule* and *C.glaucum* yields a t- value of 28.48, which is . significant at the 0.001 percent level.

Fig 7 - Regression lines with 95% confidence limits for C.edule and C.glaucum from the Crouch mixed cockle population.

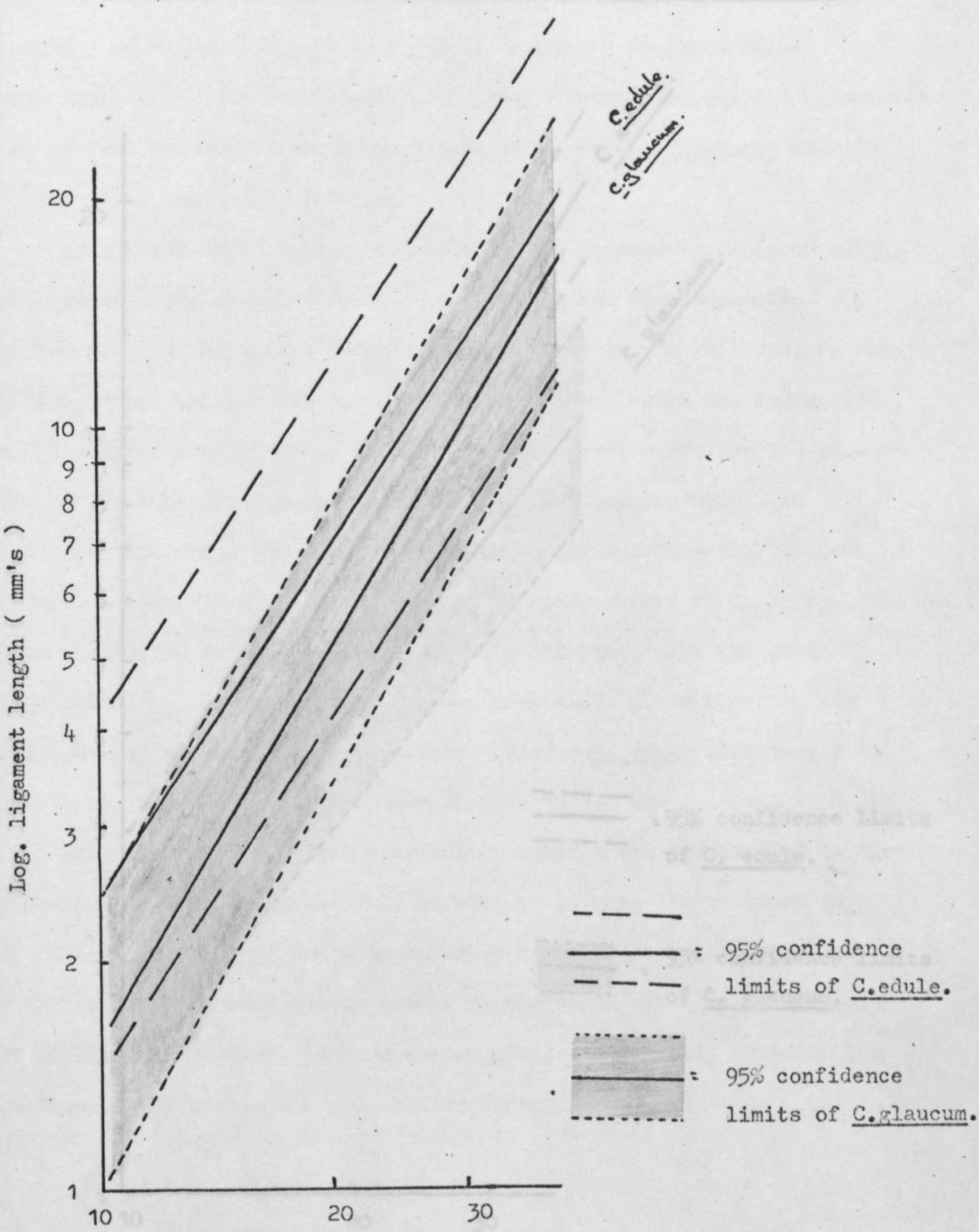
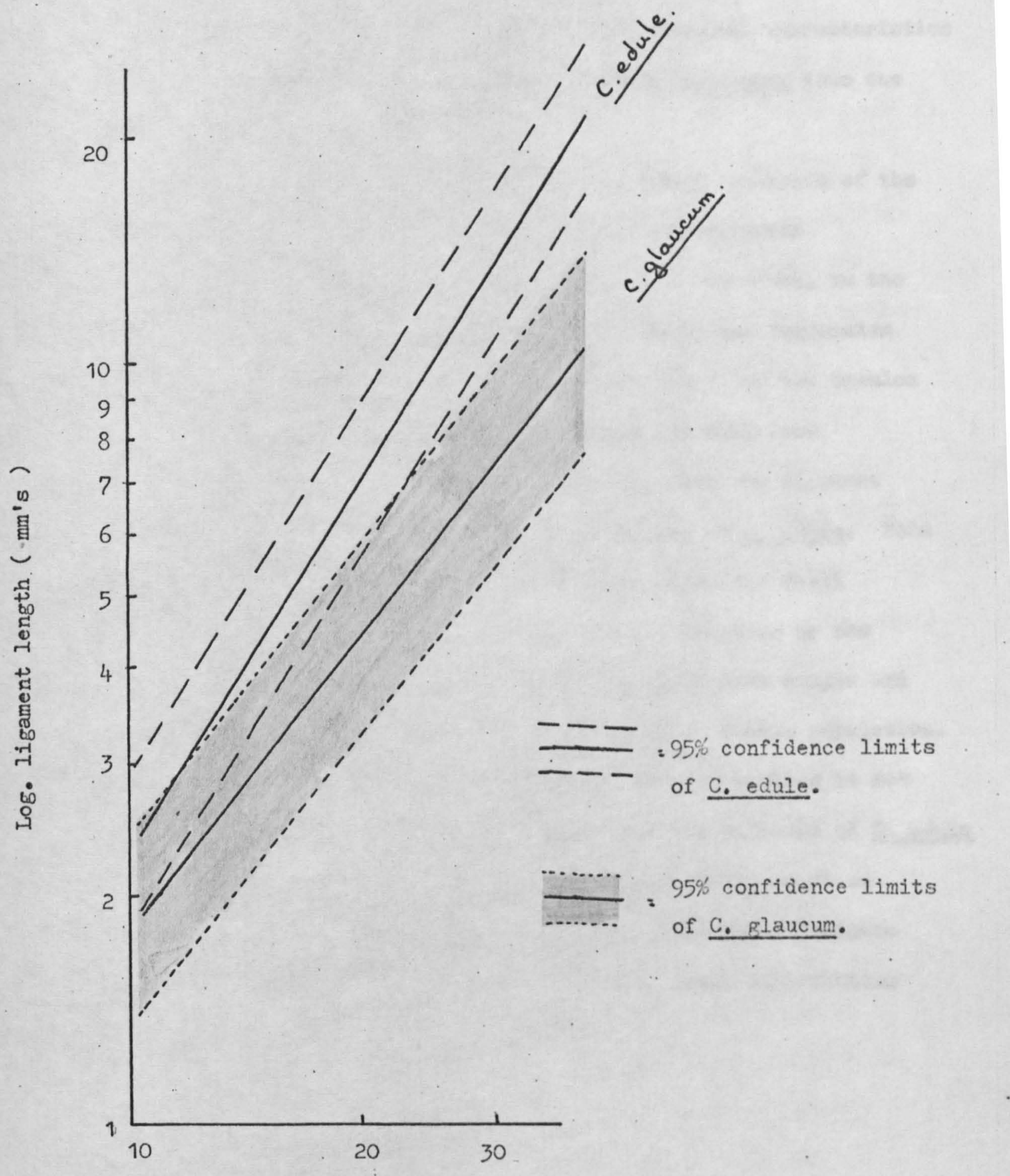


Fig 8 - Regression lines for separate cockle populations of C.edule and C.glaucum together with 95% confidence limits.



These general rules thus assist in isolating certain individual cockles as being either C. edule or C. glaucum, and can confirm whether the sample represents a mixed population. However, in these mixed populations, it is the consideration of several morphological characteristics which is the most effective means of separating the Cerastoderma into the two types C. edule and C. glaucum.

As has been shown above, considering the regression analysis of the log. ligament length/shell breadth data, in cockles from separate populations, discrimination between the two forms can be achieved, as the 95% confidence limits, although overlapping, do not cross the regression line calculated for the other cockle type. However, where the two cockles occur together in mixed populations, the differences are much less pronounced. It would thus seem that in these environments the ligament length/shell breadth ratio of C. glaucum approaches that of C. edule. This may be considered to be evidence of habitat influence upon the shell morphology of C. glaucum. Also, the variance differs, as shown by the width between the 95% confidence limits, between C. edule from single and mixed cockle populations, being much greater in the mixed cockle population. It may well be that biological competition between the two cockles is not important in the mixed population, because if it were the variance of C. edule (and also of C. glaucum) would be expected to be narrower in the mixed population compared with single cockle populations. This could indicate that physical or chemical factors are regulating the cockle distribution more than purely biological competition factors.

2. An attempt to quantify the posterior elongation of the shell of C. glaucum compared with C. edule.

The shell in C. glaucum is typically elongated posteriorly in contrast to C. edule which attains, in smaller cockles up to about 24mm. shell breadth, a degree of anterior-posterior symmetry, (see plates 1 and 2). Glemarec (1968) separated the two Cerastoderma from the French coast by reference to the increase in posterior portion of the shell in C. glaucum. Loppens (1923) and recently Russell (1969) are of the opinion that the posterior elongation in C. glaucum is a variable character and is dependant to some degree upon the fineness of particle size of the substrate. Russell argues that young C. glaucum found suspended in vegetation are more symmetrical than those found in the substratum. Also, because this cockle is found in a wide variety of different habitats, from muddy pools to sandy fjords, he does not regard the posterior elongation of C. glaucum as a valuable taxonomic character.

However, in the British Cerastoderma examined in this study C. glaucum is elongated posteriorly and it was thought worthwhile to attempt to quantify this elongation. Live cockles were collected from single cockle populations; C. glaucum from Cuckmere Haven, and C. edule from Whitstable, Kent. These localities are typical lagoon and littoral environments respectively for the two members of the Cerastoderma.

The valve pairs were separated and only the right valve was used in this study. The valve was pressed on to a plasticine block and an impression of the shell edge thus obtained. The umbo was marked by a pin and a perpendicular was dropped from this point onto the longitudinal axis of the greatest length of the valve, see diagram 1. Thus the height of the shell from the longitudinal axis to the umbo and the

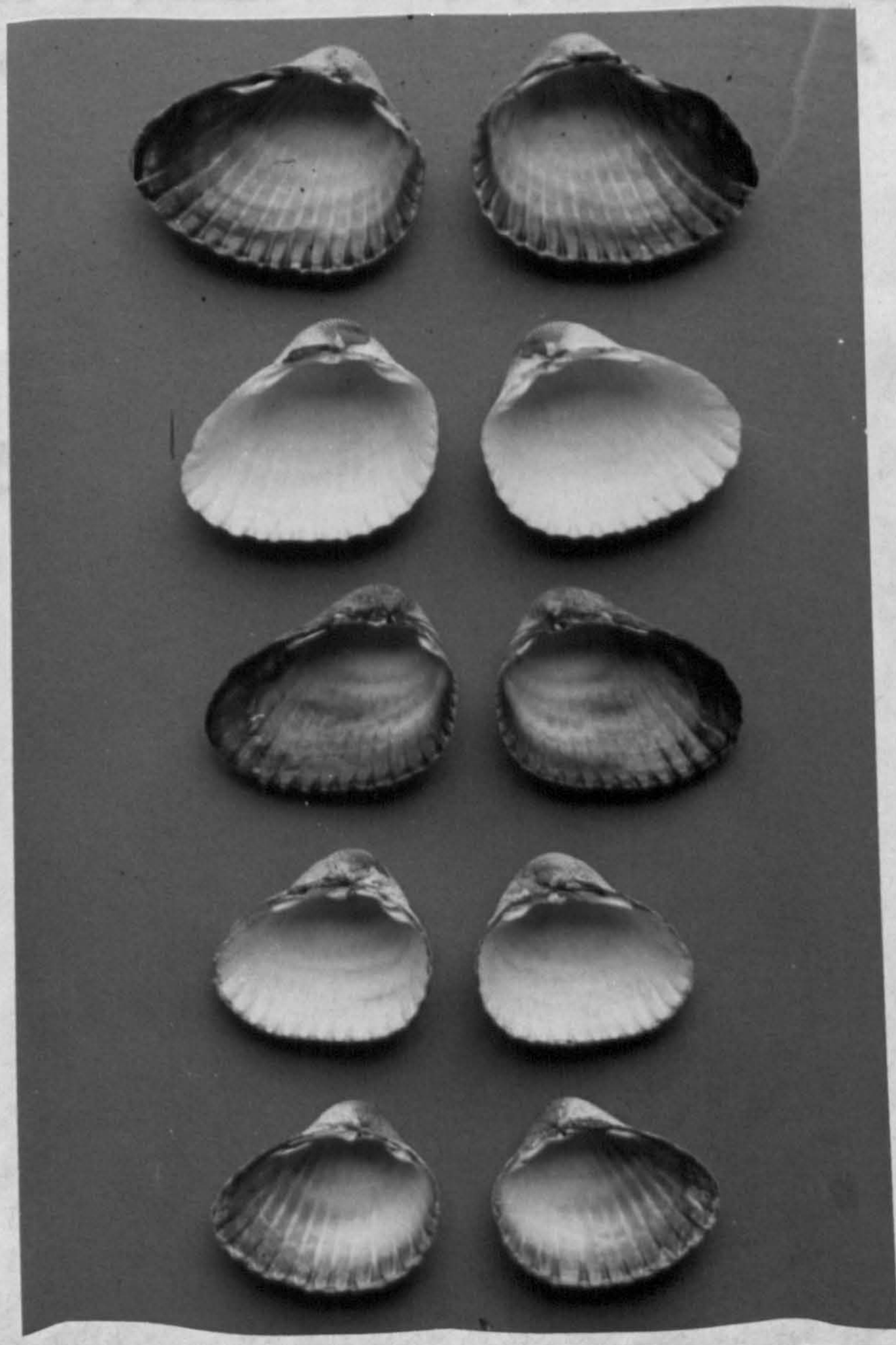
Plate 1 - Showing the posterior elongation of C. glaucum compared with C. edule. Note also the long ligament in C. edule.

C. EDULE C. GLAUCUM

Plate 2a) - Showing the asymmetry of C. glaucum and the absence of internal pigmentation in some individuals.

Plate 1

Plate 2a)



Plates showing the internal shell pigmentation of C. edule and C. glaucum.

Plate 2b) - C. GLAUCUM

C.EDULE

Note the presence of a single purple stain in all C.edule, but a variable degree of pigmentation in different individuals of C.glaucum.

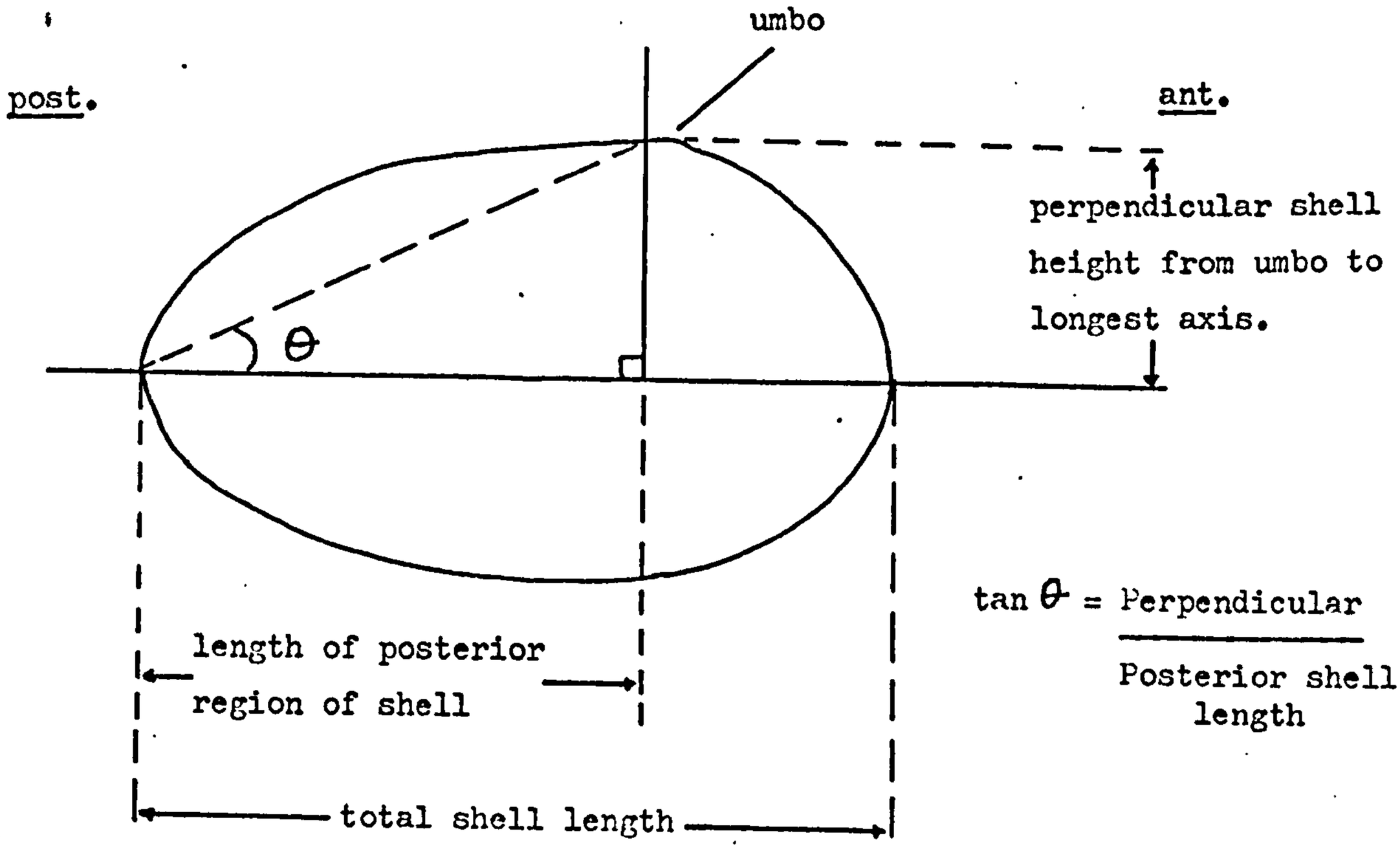
Plate 2c) -

C. EDULE **C. GLAUCUM**

Plate 2b)

Plate 2c)

Diagram 1 - Showing plasticene impression of cockle shell edge and method of determining θ.

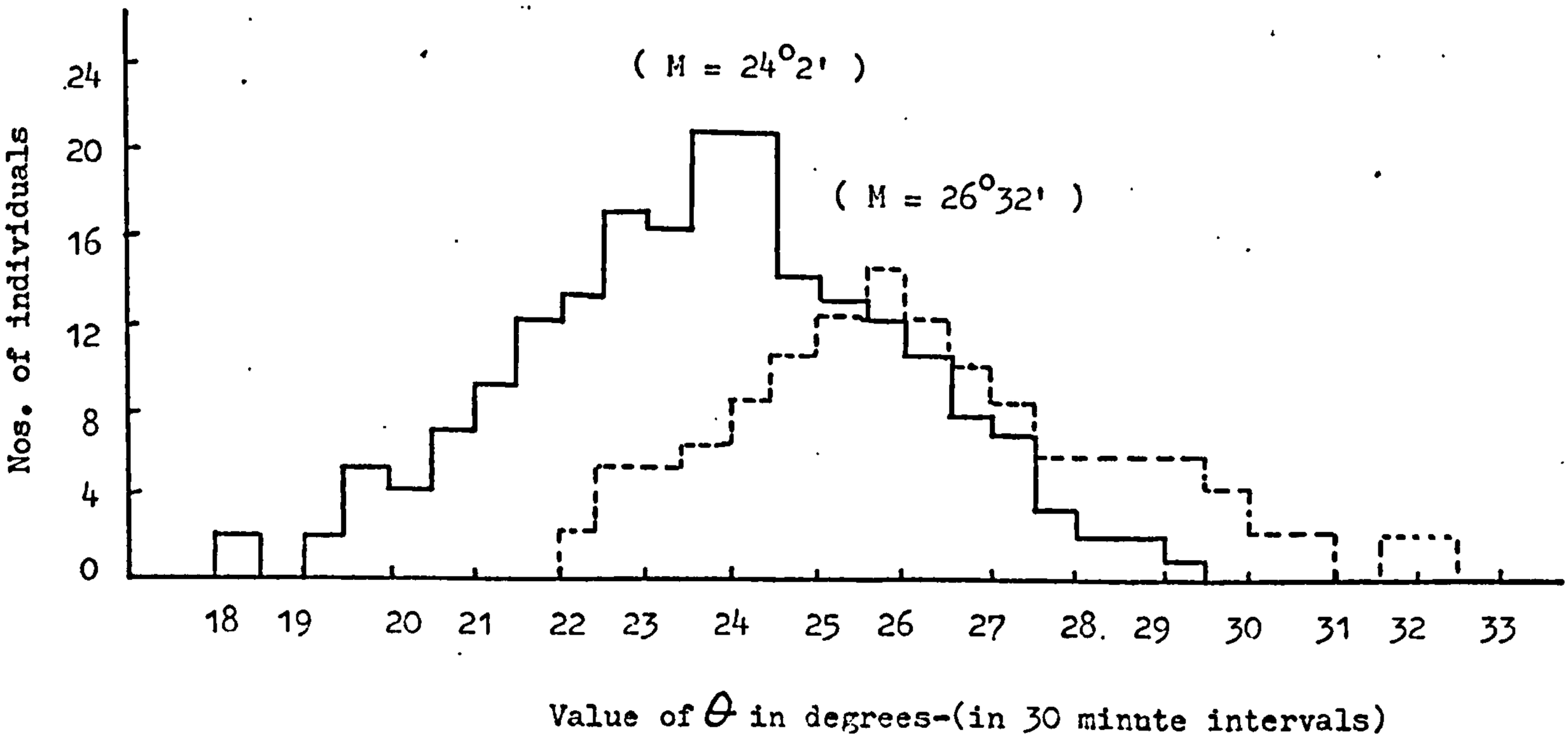


$$\tan\theta = \frac{\text{Perpendicular}}{\text{Posterior shell length}}$$

Fig 9 - Distribution of θ (see above) in two single cockle populations.

——— = 208 C.glaucum from Cuckmere Haven Lagoon

- - - - - = 125 C.edule from Whitstable, Kent

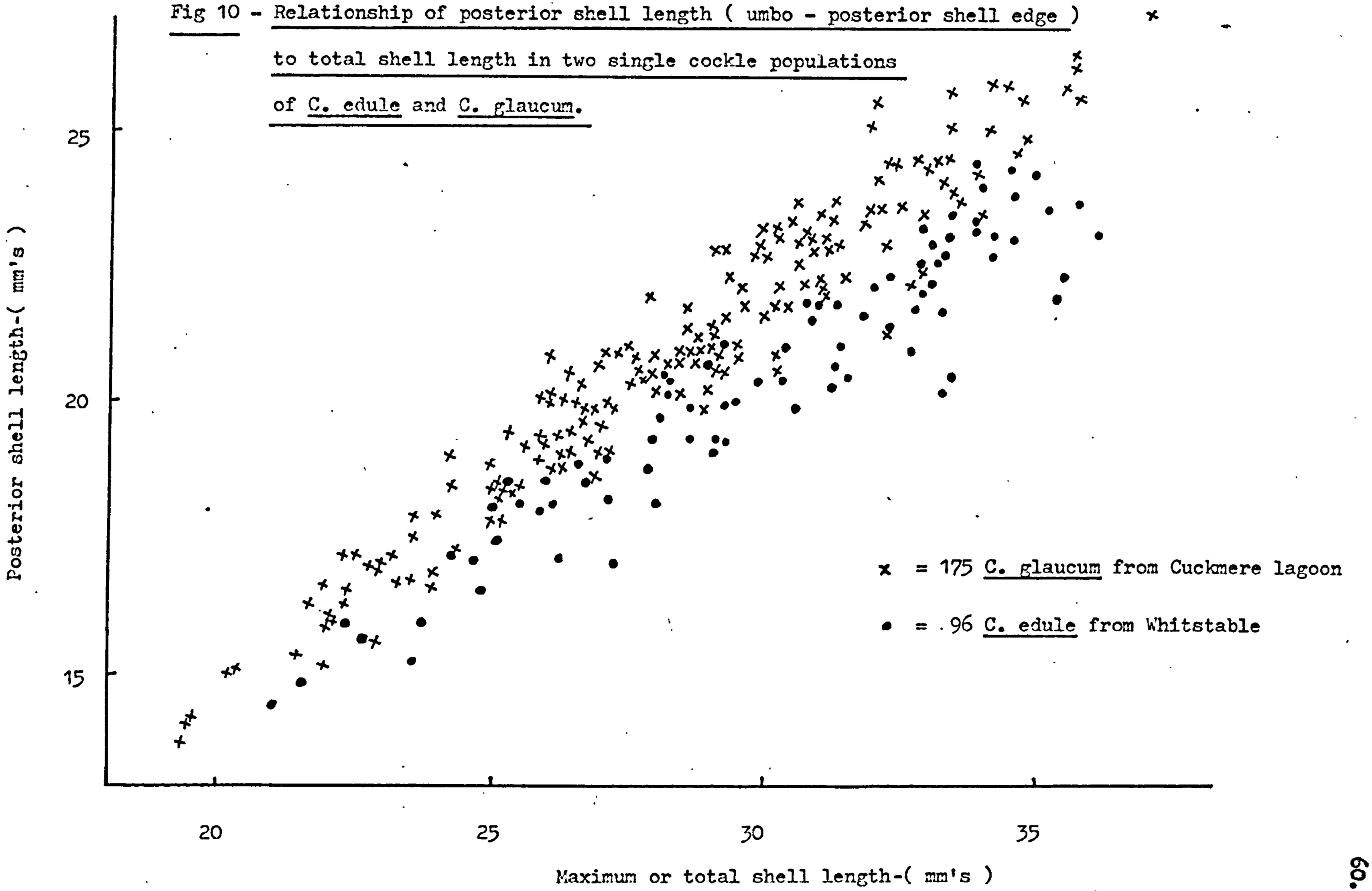


length from the umbo to the posterior valve edge along the longitudinal axis could be obtained. A value for tan the angle θ quantifying the posterior elongation could thus be obtained.

The distribution of θ for the typical C. edule and C. glaucum populations are shown on fig. 9. It can be seen that the measure of asymmetry, as quantified by the above method, is of no value in separating single cockle populations of C. edule and C. glaucum, as the distribution of θ quantifying the asymmetry overlaps in the two cockles.

A plot of the length of the posterior portion of the shell (from umbo to posterior edge along the longitudinal axis) against the maximum length along the longitudinal axis, is shown in fig. 10. Again successful separation of the two Cerastoderma could not be achieved by this method. It would seem therefore that although a difference in shell shape is obvious, it is extremely difficult to quantify. Purchon (1939) using different methods to measure asymmetry, also noted a great variability in the posterior elongation of C. edule var lamarcki (= glaucum), and concluded that variation in asymmetry of C. edule can best be explained as the result of variations in the environment, though genetic factors could play a part. Even taking genetic factors into consideration, as has been attempted here, the variability of the posterior elongation is so great within a single population, that no conclusions of taxonomic value can be drawn from the asymmetry of C. glaucum compared with C. edule.

Fig 10 - Relationship of posterior shell length (umbo - posterior shell edge) to total shell length in two single cockle populations of C. edule and C. glaucum.



3. Internal colouration of the shell of the two Cerastoderma.

It was noticed during the survey of the Crouch cockles, that whereas C. edule always had some purple or brown internal staining of the shell, a number of C. glaucum were devoid of such pigmentation, (see plate 2). Tebble (1966) records that the inside of the shell of C. edule is white, stained brown on and about the posterior adductor scar. Describing C. glaucum he states that the inside of the shell is generally dark or light brown, though it may occasionally be worn white. In fact, in live individuals of this latter cockle, no wearing of the innermost nacreous shell layer occurs, and the shell can appear either pure white or stained purple or brown. When present, the staining of the shell tends to be more extensive than that found in C. edule. The chocolate brown stain of the posterior shell extends around the ventral margin as a solid band of pigment. Towards the umbo the brown is replaced by a bluish hue. Several cockles displaying the internal shell colourations described, are shown on plate 2.

Of the several thousands of live C. edule shells examined from a wide variety of habitats, all were stained internally at the region of the posterior adductor scar and posterior lateral teeth, by a pale brown or chocolate brown pigment. Occasionally the brown staining extends around the shell margins and around the hinge teeth, but generally the majority of the shell remains white. More rarely, part of the internal shell can be perfused by lilac or bluish pigments.

The percentages of non-coloured, white, C. glaucum from various populations are shown in table 2. In lagoon populations the highest percentages are found at Finavarra, Eire; Brightlingsea, Essex; New England Creek, Essex; and Hermitage, Hampshire. Two of these, Finavarra and

Table 2

Relationship of pigment absence from the internal shell of C.glaucum with habitat and salinity of the environment.

Locality and type of environment.	Total number of C.glaucum examined.	Estimated summer salinity. -/ ‰	Number and Percentage of individuals with no inter-nal shell pigmentation. Number	Percentage
Crouch estuary, Essex- Mixed -	1151	-	538	46.7 %
Chapletown, Eire- " -	18	-	6	33.3 %
Poole Harbour- " -	8	-	1	12.5 %
The Fleet- Langton Herring-Lagoon	86	29.2 ‰	2	2.3 %
- Wyke Regis-(Fleet entrance)	126	33.6 ‰	3	2.3 %
Gosport, Hampshire- Lagoon -	74	28.2 ‰	2	12.0 %
Trawnagh, Eire- " -	33	26.25 ‰	1	3.0 %
New England Creek,Essex " -	130	25.3 ‰	44	33.8 %
Roose, S. Wales- " -	44	21.4 ‰	-	-
Cuckmere, Sussex- " -	148	20.3 ‰	6	3.9 %
Brightlingsea, Essex- " -	30	20.3 ‰	14	46.7 %
Hermitage, Hants.- " -	102	10.4 ‰	8	21.7 %
Finavarra, Eire- " -	11	8.7 ‰	10	90.9 %

Hermitage, are low salinity environments of 8.7 and 10.4‰ respectively. High values are also given by the Crouch estuarine C. glaucum and by the Chapletown, Eire C. glaucum from mixed populations. The fact that the percentage incidence of pure white shells varies from lagoon to lagoon may suggest that this feature is environmental rather than genetically determined. It would appear that low salinity or fresh water inflow is in some way correlated with the high incidence of pure white shells.

Loppens (1923) records internally stained shells in the Mediterranean from the Etang St. Eygulfe, and from the Adriatic Sea near Venice. However, in Mediterranean populations of C. glaucum adjacent to fresh water inflows, the shells were white. He also records white C. glaucum from the Caspian Sea, living in low salinity environments of 0.7 - 13‰ salinity, and from the entrance to the Baltic Sea. Bateson (1889) studying cockles on terraces above the Aral Sea , concluded that as the salinity increases, the internal shell becomes more highly coloured. It would seem therefore that internal shell pigmentation is correlated with salinity, the higher the salinity the more coloured the shell. C. edule does not occur in waters less saline than 16.3‰ (see Section V-3g), and the shell is always coloured. However, in the Crouch mixed population, in the same environment 47.6% of C. glaucum ~~are~~ were un-pigmented, which suggests that the factors controlling shell pigmentation differ in the two Cerastoderma.

If individuals with no internal shell pigmentation are met in a cockle population, then C. glaucum is present.

(For references see page 127.)

SECTION - III

SECTION III

DISTRIBUTION OF THE COCKLES C. EDULE (L) AND C. GLAUCUM (POIRET) IN THE BRITISH ISLES

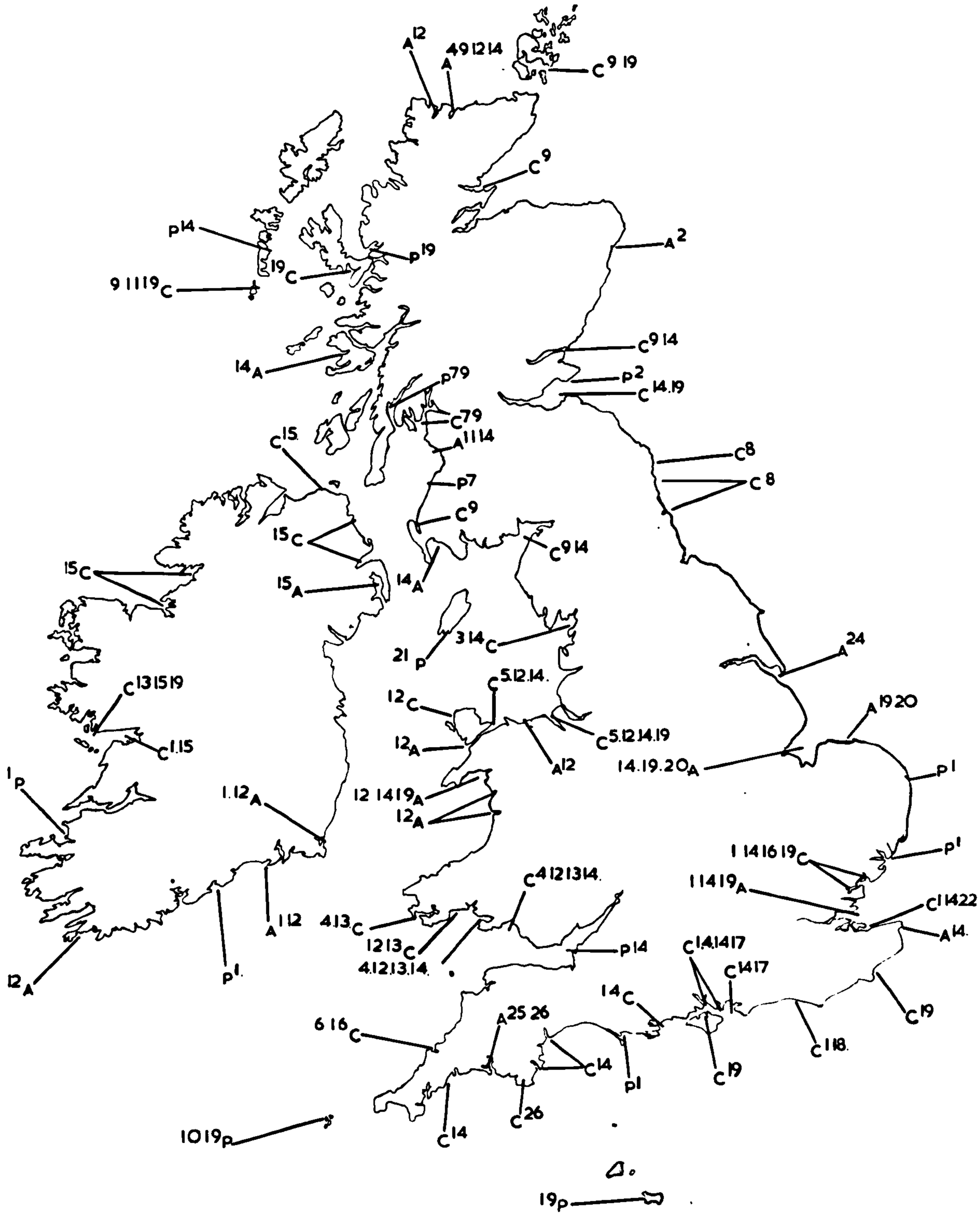
1. Distribution of Cerastoderma edule (L)

The distribution of the common cockle Cerastoderma edule is well known (see map 1 and Appendix IIA). It occurs abundantly around all the British Isles coasts; its presence being seemingly most regulated by the availability of suitable substratum for settlement. However, it occurs in a wide range of particle grade size substrates which vary from very small particles (soft mud) e.g. Chalkwell Coze, Essex, to medium grade sand, e.g. low water mark at Minnis Bay, North Kent.

This cockle forms dense populations on intertidal mud flats and these are often commercially exploited, e.g. Llanrhidian Sands, South Wales, Na/plin Sands, Essex; and the Wash, Lincolnshire and North Norfolk coasts. Commercial cockles are also farmed from several Scottish estuaries, one of the most notable Scottish cockle populations being found at Barra, Outer Hebrides. It would seem that the largest cockles are found where marine, oceanic influence is greatest, e.g. the western and northern coasts of Scotland, (Cole, 1956) for example Barra cockles, and south-west England, e.g. Portland (personal observation); see also Jeffreys (1863), and Johnston (1898).

Cerastoderma edule is recorded in most of the fauna lists produced by marine laboratories of Great Britain, and has been shown to occur commonly even in the western coasts of Eire by the author. Therefore, the distribution of this cockle, though non-continuous, is very wide, embracing all the British Isles' coasts.

MAP-I



Distribution of C. edule around the British Isles

—Legend see Appendix II

KEY

RELATIVE ABUNDANCE OF C.EDULE.

A—Abundant.
C—Common.
P—Present.

2. Distribution of Cerastoderma glaucum (Poiret)

Cardium rusticum Chemnitz (1782) (NOT Linnaeus) was the name given by early English taxonomists to cockles of the Cerastoderma glaucum type. Forbes & Hanley (1853) describe C. rusticum (Chemnitz) from the Hastings area, Sussex, and salt water marshes of Hampshire; from the Isle of Great South Arran, Galway Bay, Eire; and from the Murray Firth, Scotland. The cockles from the Arran Isle were evidently juveniles, found creeping in the masses of Confera (Chaetomorpha) crassa which abounded in the lake. This characteristic is synonymous with the known behaviour of C. glaucum in lagoons, the young often being found suspended in Chaetomorpha before they drop to the bottom to continue development to adult size. The mobility of C. glaucum in contrast to C. edule was one of the first observed behavioural differences between the two cockles. (Høpner-Petersen, 1958; Muus, 1968).

The original type description of Cardium lamarcki (= Cerastoderma glaucum) by Reeve (1845) was made from a single specimen collected from Kingsbridge, South Devon. There has since been no record of C. glaucum from the Devonshire coast. Cardium edule var. lamarcki Reeve is described by Ellis (1932) from Widewater lagoon, Shoreham-on-Sea, Sussex and the Cardium species noted by Thorpe (1927) from the Midrips and Wicks seepage pools, near Rye, Sussex, have been shown by Russell (1969) to be C. glaucum. Howes (1939) records C. edule var. lamarcki from New England Creek, Essex. Examination of this creek by the author has shown these cockles to be typical lagoon C. glaucum, whilst Purchon (1939) also describes these cockles from a seepage pool at Bawdsey, Suffolk.

More recently Cerastoderma (Cardium) glaucum localities have been recorded by the Conchological Society of Great Britain. For these I am

grateful to Mrs. S.M. Turk, the Marine Census recorder for the Society. This cockle has been collected by the Society from a small, brackish water lagoon near Coalhouse Point, Tilbury in 1963, and dead shells were received from Hyde, Isle of Wight in 1967. The Fleet, Dorset, contains a population of these cockles (Russell - personal communication 1968), as does the 'ox-bow' lake at Cuckmere Haven, near Seaford, Sussex. (My thanks to Miss J. Chatfield for informing me of this locality). R. Haxmond (1969 written communication) conveyed information concerning a lake, Salt Hole, at Holkam, North Norfolk which contains large C. glaucum; and the boating lake 1½ miles to the east of Wells-next-the-sea, called 'Abrahams Bosom', which also contains a population of this cockle. (See also Featherstone, 1968).

Tebble (1966) reviewed the distribution of Cerastoderma lamarcki (= glaucum) Reeve in British waters and considered that the cockle was 'fairly common in brackish waters between the Wash and Dorset, and that records suggest it occurs in the British Channel and Ireland.' His figure 55 (p. 105) shows single valves of both C. lamarcki and C. edule collected from the same station in the River Roach estuary, whilst figure 54 (p. 104) shows C. lamarcki collected from Pagham, Sussex. Bowden and Heppell (1968) list two localities for Cerastoderma glaucum (Poiret) from lochs in North and South Uist, in the Outer Hebrides, Scotland.

Specimens submitted to the shell collection of the British Museum, Natural History section have been examined (see Appendix I for re-appraisal of the taxonomic labelling of these cockles) and the locations of those whose morphological characteristics agree with C. glaucum are listed overleaf:

1. Portsea, Hampshire (= cockles collected from Hampshire marshes referred to by Forbes and Hanley, 1853).
2. Aberdour, collected 1843, from Fife, Scotland.
3. New England Creek, collected 1939 by G.M. Spooner (see Howes, 1939).
4. Hastings, Sussex.
5. Reculver, North Kent. (Two thick shelled valves).
6. Jury's Gut, Kent/Sussex border, collected 1937.
7. Tilbury, Essex - Coalhouse Point. 1962 (See Conchological Society).
8. Walton-on-Naze, Essex. (Donated by Miss J. Chatfield - Reading University).
9. Brackish water ditch at Aldeburgh, Suffolk.
10. Near Pevensey Bay, Sussex (dead shells).
11. Dunwich saltings pool, Suffolk, collected by H.A. Cole, Director of Lowestoft Fisheries Laboratory, Lowestoft, Suffolk.
12. The Solent area.
13. Galway Bay, Eire (one thick-shelled individual).
14. St. Nicholas Marshes, Kent.
15. Shingle street, lagoon - O (according to lagoon classification of Cobb (1956)) collected by Miss J. Chatfield.
16. Cuckmere Haven collected by Miss J. Chatfield.
17. Brackish water lake at Southwold, Suffolk.
18. Bradwell, River Blackwater Estuary, Essex. (One C. glaucum amongst an assortment of C. edule collected from the foreshore at Bradwell, by D.S. Davis, 1965. He has also donated some small thin shelled individuals collected from a settling tank at Bradwell Power Station in 1967, which may be C. glaucum.

19. Dengie marshes, Essex, north of Burnham-on-Crouch, collected from a dried up ditch (Ordinance Survey map no. 162, grid ref. 030987) inside the sea-wall, halfway between St. Peters Head and Holiwell point at the mouth of the River Crouch. Collected by D.A. Hancock, Burnham shellfish laboratories, Burnham-on-Crouch.

Some of the specimens in the above collection list were isolated dead shells, and thus it would be dangerous to base too much upon their reliability, when describing the distribution of C. glaucum. However, the majority were collections of complete, thin-shelled, valve pairs from living or recently dead cockle populations. Cockles collected from lagoons and seepage pools are invariably thin-shelled, and thus the environment of the Museum thin-shelled British C. glaucum can be assumed fairly safely to be lagoonal in nature.

If C. glaucum occurs in situations which are more marine in nature, then the shell of the cockles are much thicker. Thus the C. glaucum from the estuary of the River Roach are thick shelled, as are the cockles collected from pools which are regularly replenished by water at spring tides, e.g. Aughish, Galway Bay, Eire (see - Field studies in Western Eire). The single thick shelled C. glaucum from the Blackwater estuary was collected by D.S. Davis from a littoral location. Thus it can be tentatively assumed that the thick shelled specimens of this cockle from Reculver, North Kent, and Galway Bay, Eire, probably originated from either frequently renewed, marine pools, or littoral locations.

Russell (1969) surveyed the cockle populations of the Fleet, Dorset, and other lagoons at Winchelsea, Pagham, Midrips and Wicks, Sussex and at Horsey Island lake, Portsmouth, Hampshire. A drainage ditch at

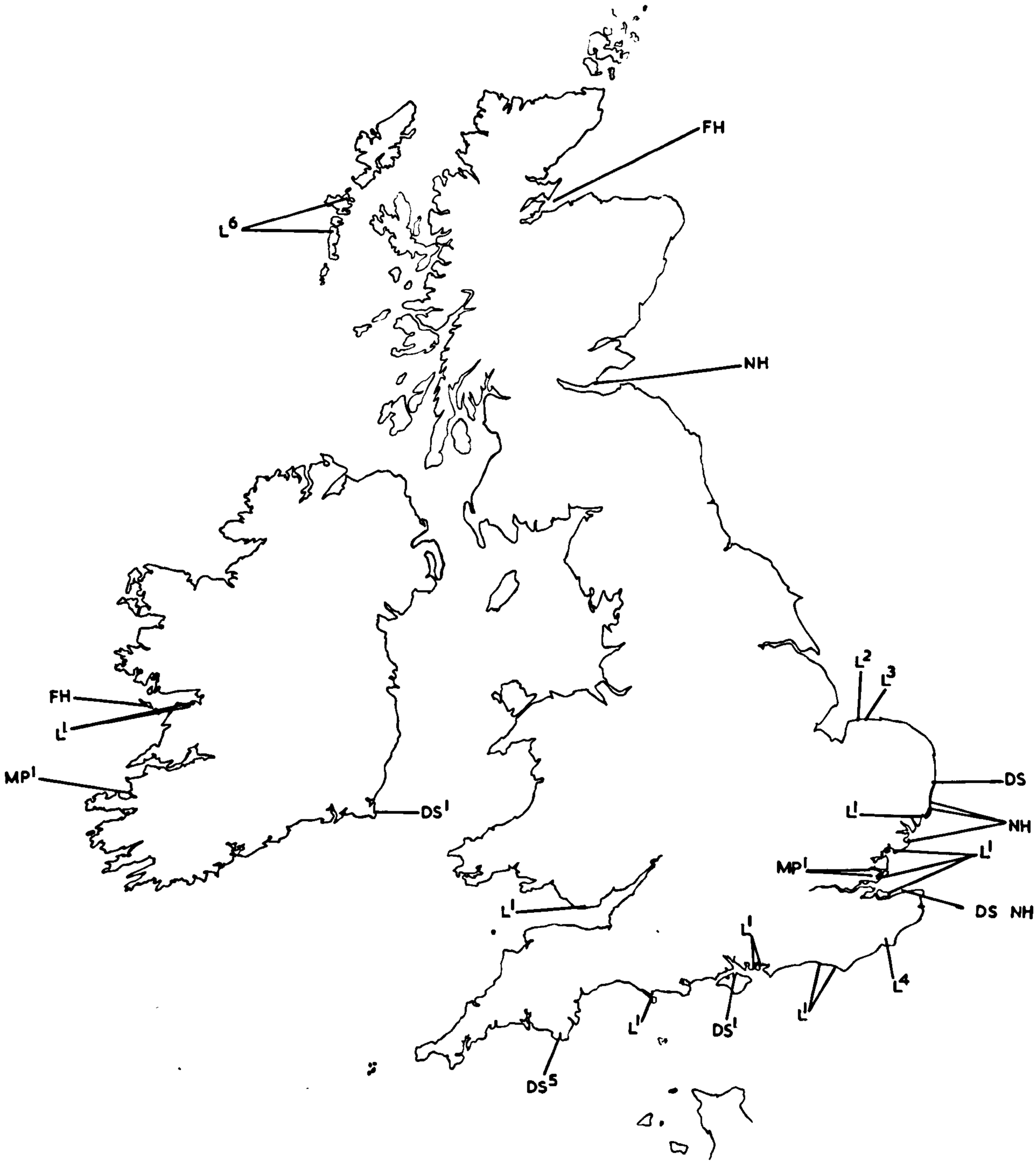
Aldeburgh contained this cockle as did seepage pools at Dunwich and between Orford Haven and Bawdsey, Suffolk. Lastly, the two lagoons at Holkam and Wells-next-the-sea were also shown to harbour populations of C. glaucum.

The majority of the above information has been accumulated over a period of three years and was not available at the outset of this research. This information together with some other localities investigated by the author is figured on map 2 (and Appendix II (B)). This map does not, however, include several sites from western Eire discovered in the summer of 1970.

To determine fully the environment and distribution of the Cerastoderma, extensive field work was conducted and is recorded in the following section.

(For references see page 127.)

MAP-2



Distribution of C. glaucum around the British Isles

—Legend see Appendix II.

KEY

FH — Forbes & Hanley(1853).

NH — In Natural History Museum Collection.

DS — Dead Shell localities.

L — Lagoon sites.

MP — Mixed Population of C.glaucum & C.edule.

SECTION - IV

SECTION IV

FIELD INVESTIGATIONS TO DETERMINE HABITAT AND DISTRIBUTION OF C. EDULE AND C. GLAUCUM

1. Field studies in south-east England

An initial objective of this work was to determine the distribution and habitat preferences of Cerastoderma edule and Cerastoderma glaucum in south-east England. Both cockles are recorded in this region by Tebble (1966), and a study was made of the environment where each cockle type occurred. Høpper-Petersen (1958) considered C. lamarcki (= glaucum) to be a brackish water cockle and this was also the view of Tebble (1966) and Muus (1968). Thus, salinity was regarded as one variable which could be important in regulating cockle distribution, and was therefore monitored at each cockle locality. This was measured in the majority by a hydrometer (specific gravity range 1.000 - 1.030) and in later field work by a portable 'Dionic' conductivity meter. The salinity of standard salt solutions was related to conductivity units (c.u.'s) to calibrate the meter. Other environmental parameters such as temperature and p.H. because of their great variability were considered to be less likely factors affecting distribution of the cockles. A brief description, stating whether littoral, seepage pool or lagoonal location, was made for each site, and note made of the substratum present and some of the associated fauna and flora. Aerial exposure was quantified, whenever this was relevant, with reference to the number of hours that cockles were exposed to air in every 12 hours and converted to percentage exposure.

estuaries, Essex. In these populations the ratio of the two cockle types was in the region of 50:50 and 20:50 respectively. A survey of the cockle distribution in the region of these estuaries can be found at the end of this section. Other mixed populations occurred on the shore of Horsey Island, and Hermitage, Portsmouth. These two later populations were predominantly C. edule with a few C. glaucum near low water mark, amounting to a maximum of in the region of 10% of the total cockle population. A sample of 30 cockles collected from Horsey Island fore-shore by Mr. P. Steadman contained three C. glaucum, whereas subsequent visits to this site did not yield any C. glaucum. At Hermitage a few C. glaucum occurred on the shore in 1968 beneath the sluice gates running from a swimming pool. This pool contained a population of C. glaucum when examined in 1968 and presumably larvae from this population could have been swept out of the pool and subsequently settled on the foreshore. Moreover, they occur directly adjacent to this pool in a channel containing water for the majority of the tide and are therefore seldom exposed to air.

Isolated specimens of C. glaucum have been collected from the shore and are listed below:

1. Individual in a littoral channel at Tollesbury, Essex.

   At Tollesbury is a temporary lagoon site which has been recorded to contain C. glaucum and therefore this solitary specimen could well have been derived from this lagoon stock.

2. Single individual from Poole Harbour, Dorset, collected by G. Pickett (Burnham Shellfish laboratory, Burnham-on-Crouch). The presence of C. glaucum in Poole harbour has been further substantiated (see later).

3. Single specimen from Whitstable, Kent, collected by the author in the winter of 1968 from the intertidal mud flat.

4. A single individual C. glaucum was found in a sample of C. edule in the British Museum, Natural History section. This had been collected from Bradwell foreshore, in the Blackwater estuary, by D.S. Davis. (See earlier - Section III).

All these isolated records of C. glaucum are from shore localities where there is some exposure to air during periods of low tide. The rareness of these individuals discounts the hypothesis that there is a range from C. edule type to C. glaucum type on the shore and suggests that some factor or factors prevent settlement and subsequent colonisation of the shore by C. glaucum. The more extensive intertidal populations of C. glaucum at Portsmouth and Poole and the Rivers Crouch and Roach, Essex, have in common the fact that all are extremely sheltered localities being seldom exposed to wave-action, and this may be important in the maintenance of these shore populations.

(i) The distribution of Cerastoderma edule and Cerastoderma glaucum in the neighbourhood of the Crouch and Roach estuaries, Essex.

Tebble (1966) recorded both members of the Cerastoderma from the same station in the Roach estuary, and both cockles were also stated to occur in the Crouch estuary by scientists from Burnham Shellfish Laboratory, Burnham-on-Crouch. A survey of the cockle populations in these estuaries was conducted, and the presence of either cockle type was also noted in the neighbouring areas of the Essex coast. This survey was conducted from the shore at low water spring tides, whilst observations on the cockle distribution in the upper reaches of the

Roach estuary was also conducted by boat dredge. (The boat for this work was kindly supplied by Burnham Shellfish Laboratory). Cockle abundance was graded into three arbitrary categories:- Abundant, Common and Present.

The results of this survey are shown in figure 1. C. edule is found widely distributed along both estuaries where the substrate is suitable for settlement; from Hullbridge Ferry downstream in the Crouch estuary, and from 'Broadrakes' downstream in the Roach estuary. C. glaucum on the other hand occurs only in populations at the heads of both estuaries, and in the New England Creek lagoon system.

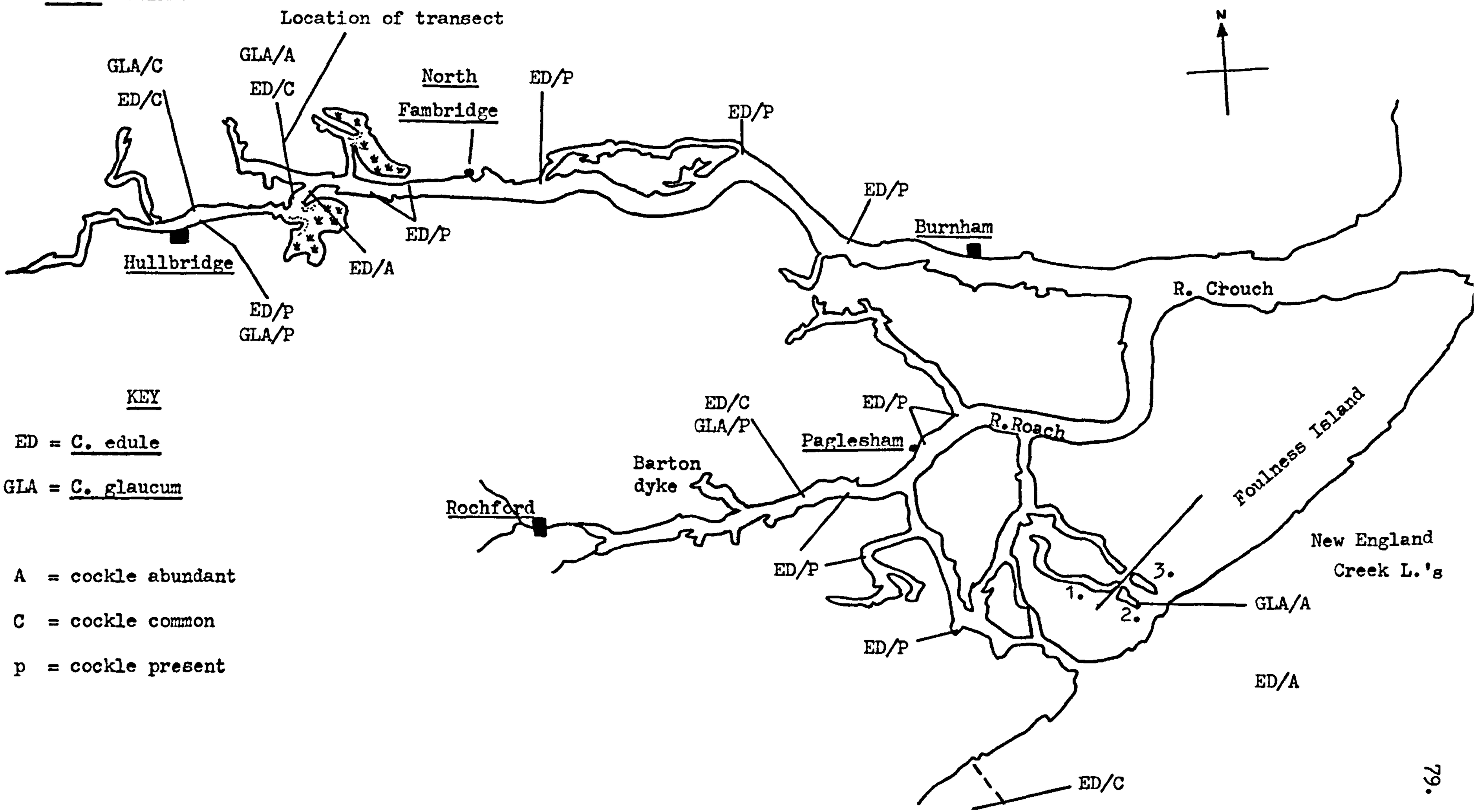
The estuarine C. glaucum are thick-shelled individuals, the weight of the shells being similar to C. edule from the same environment. (See Section V, fig. 21). The fact that lagoon populations of C. glaucum are invariably thin-shelled (as are the New England Creek cockles) does allow conclusions to be tentatively drawn upon the environment of shells which have been collected, but details of the exact location omitted. (See Appendix I).

The presence of C. glaucum populations in the uppermost regions of the Crouch and Roach estuaries is of interest. It was recognised that water was retained in the Crouch estuary even at low tide, and that this may be important for the maintenance of the population. Also, both the Roach and Crouch localities are sheltered from wave action and this may very well be an important contributory factor.

(ii) Geological explanation for the presence of C. glaucum in the Crouch and Roach estuaries

The absence of populations of C. glaucum in other estuaries of the south-east, especially other estuaries of Essex and Suffolk, can be

Fig 1 - Distribution of Cerastoderma edule and C. glaucum in the estuaries of the Rivers Crouch and Roach, Essex.



KEY

ED = C. edule

GLA = C. glaucum

A = cockle abundant

C = cockle common

p = cockle present

explained on the basis of the exceptional geological characteristics of the Crouch and to a lesser extent the Roach. With the close of the glacial period of Pleistocene times the physiography of Essex must have been similar to the present pattern (Coles, 1936). Thus the Crouch approximated to the southern limit of the ice sheet of this glacial period. Melt water from the ice probably drained into the Crouch headwaters, which may explain in part the depth of this estuary. In contrast, the ice had gouged deep 'V'-shaped estuaries in northern Essex, which had been reinforced by copious melt water from the receding ice sheet. This type of river profile of northern Essex is in direct contrast to the broader 'U' shaped valleys of the Crouch and southern estuaries. Thus Coles recognised young river profiles in the more northern Essex rivers, but a more mature profile in the Crouch estuary. In the Crouch longitudinal profile there are also pronounced 'knick points' associated with sharp change in the river profile. (Coles, 1936; Greensmith & Tucker (1970 - Proc. Geol. Assoc. in preparation)). A 'knick point' is particularly prominent downstream of Hullbridge ferry and this together with the fact that the estuary is wide at Brandy Hole (see fig. 1) results in water being retained at low tide.

It is suggested that this water retention in the estuary at low tide (see plate 1) is sufficient to account for the presence of C. glaucum, an otherwise lagoon cockle, in the Crouch estuary. Indeed, the exposure to air of this population is not great. The maximum aerial exposure during spring tides is c. 2 hours/12 hours (16% exposure to air) and it has been estimated that the Crouch cockles are not exposed at all during neaps for about 62 tides/100 tides. On the other hand, the estuary is moderately deep and fast flowing, resulting in a strong tidal flow at Hullbridge. Thus, some aerial exposure and swift tidal movement occurs

Plate 1

Plate 2

Plate 1 - A photograph of the River Crouch looking upstream towards Hullbridge ferry, showing the retention of water in the middle estuary at low tide.

Plate 2 - A typical sample of cockles containing both Cerastoderma types from the Crouch mixed population at Hullbridge.

at the region of the mixed cockle population, and these environmental qualities are regarded as essential requirements demanded by C. edule.

(iii) Description of the two mixed cockle populations in the Crouch and Roach estuaries.

Therefore two mixed Cerastoderma cockle populations occur in this region. The Roach mixed population is found in mid-estuary, where water is retained, from Barton Dyke to Broad Rakes. Only C. edule was noted in Paglesham Reach and below. The extreme of this mixed population can be reached from the shore at Barling Marsh, however, mainly C. edule occur on the shore in this region. It is of interest to note that some individuals collected from this mixed cockle population are intermediate, as regards to shell characters, between C. edule and C. glaucum. This fact, together with the apparent smallness of the population suggests that incomplete separation between the two forms occurs in this population, and may well result in the extinction of one cockle type.

The Crouch mixed population is more extensive. The modern upstream limit of cockles is at Hullbridge 'ferry' (ford). Local information suggests that cockles could be found in earlier years well above the ferry, but presence there now is probably prevented by pollution.

At low spring tides, C. glaucum and C. edule can be collected in numbers from the northern shore about one kilometre downstream of the ford. All comparative work reported later was conducted upon animals collected from this population. A typical sample of cockles from this population is shown in plate 2. The southern shore is less populated with cockles but individuals of both kinds can be gathered. Downstream, opposite Brandy Hole Yacht Club, the shores on both sides of the river

become gravelly and unsuitable for cockle settlement. Banks of dead shells are common here as they are at Hullbridge 'ferry'. At Brandy Hole the river turns north-eastwards and broadens. Here mud returns as substratum and a mixed population of the cockles occurs again on the northern shore. C. glaucum is very common, probably more so than is C. edule. On the southern shore C. edule is the most common cockle and is very abundant, C. glaucum occurring nearer the low water mark. At Clemenisgreen creek C. glaucum abruptly dies out and only a few individual C. edule are found on the shore downstream towards North Fambridge. The separation of the Crouch cockles into two types using the shell characteristics of Høpner-Petersen (1958) is almost complete, although a few intermediate individuals do occasionally appear. The Crouch mixed population is extensive and this has allowed a comprehensive comparative study to be made between the two cockles. The populations of both types seem to be thriving, and judging by the abundance of dead shells of both cockles, has been in existence for some time.

Regular sampling of the Crouch population was conducted during 1968 and 1969, and salinities of the environment determined at Hullbridge ferry at the extreme limit of the cockle populations. Later, salinities of water collected from above the middle of the cockle population about 0.5 miles downstream, were also measured. The variation of salinity of the Crouch and Roach is shown in table 1. Samples were made predominantly at low tide after collection of cockles from the shore. The salinity of the water in winter was reduced to almost fresh water, but this was only temporary, the salinity increasing substantially with the turn of the tide. During the majority of the year the range of salinity was between c. 5 - 30‰. Burnham Fisheries laboratory monitored salinities at

Table 1 - Salinity measurements obtained for the Rivers Crouch and Roach, Essex.

Salinity of the Crouch at Hullbridge Ferry from 1968 - 1969.

Date of sample	Sample location	Specific gravity or conductivity units & salinity‰		Water temperature °C.	State of tide
22.4.69.	Collected above cockles	1.0090	10.5‰	9.5°c.	Low tide
" "	Hullbridge Ferry	1.0065	7.25‰	10.0 °c.	Low tide
4.5.69.	Collected above cockles	1.0120	15.25‰	15.25 °c.	Tide running in strongly
" "	Hullbridge Ferry	1.0060	7.5‰	15.25°c.	Low tide
10.5.69.	Collected above cockles	1.0110	13.5‰	13.0 °c.	Low tide
" "	Hullbridge Ferry	1.0090	11.0‰	13.0°c.	Low tide
29.5.69.	Collected above cockles	1.0090	10.8‰	12.5°c.	Low tide
" "	Hullbridge Ferry	1.0055	6.3‰	12.5°c.	Low tide
5.6.69.	Collected above cockles	1.0115	14.25‰	13.0°c.	Low tide
15.6.69.	Collected above cockles	1.0145	19.3‰	19.0 °c.	Low tide
" "	Hullbridge Ferry	1.0120	16.3‰	19.5°c.	Low tide
14.7.69.	At Brandy Hole	1.0175	24.2‰	21.5°c.	Low tide
" "	Collected above cockles	1.0115	16.3‰	21.5°c.	Low tide
" "	Hullbridge Ferry	1.0085	11.7‰	21.5°c.	Low tide
27.7.69.	Collected above cockles	1.0160	22.1‰	21.0°c.	Tide running in.
" "	Hullbridge Ferry	1.0130	18.1‰	21.0°c.	Tide running in.
19.8.69.	Collected above cockles	1.0135	18.8‰	21.5 °c.	Low tide
" "	Hullbridge Ferry	1.0075	11.2‰	22.0 °c.	Low tide
26.8.69.	Collected above cockles	1.0145	16.8‰	13.5 °c.	Tide running in
" "	Hullbridge Ferry	1.0095	11.7‰	13.5 °c.	Tide running in.

Table 1 - continued

Date of sample	Sample location	Specific gravity or conductivity units & salinity.	Water temperature °C.	State of tide
21.5.68.	Hullbridge Ferry	1.0095	11.3‰ 12 °c.	Low tide
23.5.68.	Hullbridge Ferry	1.0070	9.0‰ 16.25°c.	Low tide
30.5.68.	Hullbridge Ferry	1.0100	12.75‰ 15.75°c.	Low tide
6.6.68.	Hullbridge Ferry	1.0130	17.3‰ 18.5 °c.	Low tide
13.6.68.	Hullbridge Ferry	1.0165	22.0‰ 19.25°c.	Tide running in
19.6.68.	Hullbridge Ferry	1.0080	11.5‰ 21.0°c.	Low tide - surface water
" "	Hullbridge Ferry	1.0115	15.75‰ 19.75°c.	Low tide - water from 2.5' depth
26.6.68.	Hullbridge Ferry	1.0135	17.75‰ 17.25°c	Low tide
30.6.68.	Hullbridge Ferry	1.0130	17.7‰ 20.0 °c.	Low tide
11.7.68.	Hullbridge Ferry	1.0130	16.4‰ 14.5 °c.	Low tide
25.7.68.	Hullbridge Ferry	1.0225	29.75‰ 18.0 °c.	High tide
" "	Hullbridge Ferry	1.0090	11.75‰ 17.0°c.	Low tide
6.8.68.	Hullbridge Ferry	1.0092	11.8‰ 17.5°c.	Low tide
21.8.68.	Hullbridge Ferry	1.0070	10.0‰ 20.75°c.	Low tide
20.9.68.	Hullbridge Ferry	1.0020	c.2.2‰ 14.0°c.	Low tide
26.9.68.	Hullbridge Ferry	1.0020	c.3.0‰ 14.75°c.	Low tide
24.10.68.	Hullbridge Ferry	1.0065	7.3‰ 11.5 °c.	Low tide
21.11.68.	Hullbridge Ferry	1.0050	5.1‰ 5.5 °c.	Low tide
21.12.68.	Hullbridge Ferry	1.0020	c.1.8‰ 6.0 °c.	Low tide
11.1.69.	Hullbridge Ferry	1.5×10^4	0.85‰ 4.5 c	Low tide
22.1.69.	Hullbridge Ferry	1.92×10^4	1.8‰ -	Low tide.
8.3.69.	Hullbridge Ferry	4.3×10^4	2.6‰ -	Low tide
7.4.69.	Collected above cockles.	1.0080	9.2‰ 9.5 c.	Low tide
" "	Hullbridge Ferry	1.0050	5.25‰ 9.5°c.	Low tide

2. Salinity of the River Roach near Paglesham, Essex.

13.5.68.	Broadrakes	1.022	27.5‰ 12.0 °c.	Mid-tide
" "	Broadrakes	1.022	27.7‰ 12.5 °c.	High tide
1.6.68.	Broadrakes	1.020	27.25‰ 20.75°c.	Low tide

Brandy Hole during 1966-7, and record a variation of 8.5 to 31.5‰. Certainly wide salinity fluctuations do occur in the Crouch. These may be accentuated in the summer by 'salinity inversions' which have been recorded in both the Crouch and Roach estuaries by Sorby (1906). Because of evaporation during the summer months the salinities of the upper estuaries may be greater at low tide than at high tide. A similar situation was recorded in 1970, after the hot dry early summer. On the 19th July 1970 at approximately the same tidal state (high tide) the following salinities were measured:

River Crouch,	Hullbridge Ferry	- 30.8‰
River Roach,	Barling Marsh	- 31.8‰
Shoeburyness,	Southend	- 28.7‰

Thus, higher salinities were recorded in the upper estuaries compared with water collected from several miles outside the estuary mouth. With the smaller volume of fresh water draining into this river, the overall salinity of the Roach is probably greater than the Crouch. The locations of the mixed cockle populations are thus typically estuarine in nature.

Similar mixed populations may well occur on the Continent. Loppens (1923) discusses thick-shelled cockles of both types from a population in the Yser estuary, Nieuwpoort, Belgium, which may have been equivalent to the English mixed populations. It is also possible that a similar population of both cockles may occur in the Rhein - Mass - Schelde estuary complex of the Netherlands, which is comparable in many ways, including geographical relationship to the Pleistocene ice sheet, as the Crouch - Roach estuaries of England.

c. Cockle populations of the Cerastoderma glaucum type only.

A list of localities of this cockle is shown below:

(i) North Norfolk

The two localities below have not been visited but have been included for completeness.

(a) Wells-next-the-sea. (O.S. map 125. Grid ref. 886.451)

At Wells is a boating lake containing Cerastoderma glaucum which has been described by Featherstone (1968). It is a lagoon cut off from the sea and is totally non-tidal. The substratum is very muddy and two associated molluscs Mya arenaria and Lepidochitona cinereus are recorded by Featherstone. The salinity varies from 13.3 - 17.5‰ (Russell, 1969).

(b) Salt Hole at Holkam Gap. (O.S. map 125. Grid ref. 912.453)

R. Hammond (1969 written communication) informed me of this lagoon 1½ miles west of Wells boating lake, which contains very large C. glaucum. Russell (1969) suggests it is fed by a salt water spring and records the salinity as 20.9‰.

(ii) Suffolk

(a) Southwold. (O.S. map 137. Grid ref. 511.769)

At Southwold, Suffolk was discovered a series of shallow, mud filled depressions adjacent to a brackish water stream, which at one time were pools maintaining small C. glaucum populations. Only dead shells of this cockle were collected. In the sides of one of these pools was a large bank of C. edule shells. These shells were abundant and almost circular in outline.

(b) Dunwich. (O.S. map 137. Grid ref. 498.743)

H. Cole (1969 written communication) informed me of the seepage pools at Dunwich, Suffolk. These lie behind a shingle ridge and are

similar to the series of pools found at Orford. Only dead shells were discovered. According to Russell these pools are subjected to periodic drying up and re-invasion by sea water which is typical of seepage pools separated from the sea by shingle ridges.

(c) Orford, Shingle Street to Bawdsey. (O.S. map 150. Grid refs. between 374.436 and 358.407)

Russell (personal communication) reported the existence of a series of seepage pools running from Shingle Street, southwards towards Bawdsey. The cockles mentioned by Purchon (1939) came from one of these sites. The seepage pools are separated from the sea and each other by shingle ridges. The substratum is soft mud overlying shingle which is found at the pool fringes. Live C. glaucum were discovered in several of these pools (lagoons 4 and 7 according to Cobb, 1956) but the populations did not seem very extensive. Dead shells of C. glaucum were quite common. For further reference see Russell (1969).

(iii) Essex

(a) Brightlingsea boating lake. (O.S. map 162 Grid ref. 082.163)

This lagoon has been separated from the sea at Brightlingsea point and reinforced by a concrete wall to retain water. The C. glaucum population is found in the extensive Chaetomorpha crassa that occurs in spring and summer, larger individuals occuring in the soft, mud bottom. The cockles were, however, small compared with other populations, the biggest collected being only c. 1.5 cms. long. This may indicate recent invasion of the lagoon or a stunted population. The latter case is usually associated with low salinity, which does not occur, and therefore, the former may prove to be the correct explanation. Included in the associated fauna are numerous Idotea viridis, Gobius minutus, Gasterosteus aculeatus and abundant Littorina saxatilis. The salinity

on the 7th May 1968 was recorded as 20.3‰ (S.G. = 1.0016 at 14.5°C), and a second visit on the 27th December 1968 gave a salinity of 23.4‰ (3.3×10^4 conductivity units - C.U.). The salinity thus seems to remain fairly high and relatively constant. The pool is non-tidal and truly lagoonal in nature, the cockles being permanently submerged.

(b) Tollesbury swimming pool. (O.S. map 162. Grid ref. 968.105)

Tebble (personal communication) reported the existence of C. glaucum in this pool. When it was examined on the 19th July 1963 no living C. glaucum were found but numerous spat size dead shells were discovered around the pool periphery. On a subsequent visit the pool had been drained through an outlet pipe. It appears that this pool is filled before the summer and left almost empty through the winter. The pool is, therefore, not a stable C. glaucum site. One C. glaucum discovered in a nearby marine dyke running into the Blackwater may well represent an individual swept out of this pool.

(c) New England Creek, Havengore Island

This creek (in reality a lagoon) is situated to the south of Foulness Island and north of Shoeburyness, Southend. In 1925 the creek, running from a tributary of the River Roach to the sea at Maplin sands, was dammed at both ends producing a marine lagoon (see fig. 1). Further information is given by Howes (1939). A road running to Foulness Island divided the creek into two lagoons, connection between the pools being afforded by a small sluice pipe. Because of low water levels no water interchange, could occur between the lagoons when the area was visited on the 28th January 1969. For permission to survey this area, I am indebted to Lt. Col. D.A.E. Carter, Ministry of Defence, Proof & Experimental Establishment, Southend on Sea, Essex.

The portion of the creek examined by Howes was the largest lagoon on the left side of the Foulness road (O.S. map 162. Grid ref. 982.893). This lagoon contained only small C. glaucum and sparse amounts of Chaetomorpha crassa. The salinity of this water was 21.6‰ (3.1×10^4 C.U.) In winter Howes found the salinity of this water in 1934 to be 21.5‰ which increased to 27.9‰ in the autumn of 1935, thus the measured salinity was almost identical in 1969 as 35 years earlier. It would thus appear that the physical conditions regulating water seepage into or out of the lagoon have remained relatively constant over this period of time.

To the right side of the road (O.S. map 162. Grid ref. 985.893) was the small lagoon section of New England Creek, effectively cut off from the previous lagoon by the Foulness road. This lagoon contained abundant C. glaucum, and a rich associated fauna (for the probable complete fauna see Howes). Chaetomorpha crassa and Ruppia maritima abounded. Within the thick, mud substratum was discovered Mya arenaria, Littorina saxatilis, Hydrobia ventrosa, Arenicola marina, and Carcinus maenas. The prawn Palaemonetes varians occurred with Gobius minutus and Gasterosteus aculeatus. This water was a little less saline 18.5‰ (2.75×10^4 C.U.'s) than the previous larger lagoon. The substrate varied from soft mud to thick clay. In these latter regions C. glaucum remained only half buried in substrate and could be easily collected.

A third small lagoon, similar in almost every respect to that above, occurred on the right hand side of the road to Selford Creek (O.S. map 162. Grid ref. 984.897). The salinity was lower, 17‰ (2.6×10^4 C.U.'s) and the population of C. glaucum was a little less extensive, than the pool mentioned above.

These lagoons appear to have remained very similar in form since 1939 when Howes described the physical, chemical and biological characteristics of New England Creek. Judging by the salinity similarity between his values and modern day measurements it would seem that some lagoons at least maintain a constancy in constituents. They do not represent highly unstable and variable environments which are degenerating from truly marine to fresh water conditions. Where a locality is natural, or at least protected from drainage and sea-defence schemes, then the habitat is far more stable than is commonly recognised.

These lagoons are thus non-tidal pools containing C. glaucum which remain permanently submerged.

(d) Maldon

Dead shells of C. glaucum were collected from Maldon swimming pool (O.S. map 162. Grid ref. 858.066), and from a small pool retained behind the sea wall just to the north of Maldon. (O.S. map 162. Grid ref. 876.078). This pool has a very soft substratum, but contained no living cockles. The dead shells probably indicate that a population of this cockle did occur at one time at this site.

(iv) Kent

Sheerness boating lake. (O.S. map 172. Grid. ref. 925.742 to 937.748).

This long, narrow lagoon of some 1.5 miles in length is retained behind a sea wall and is used as a boating lake. In summer it is choked with Chaetomorpha crassa and contains the normal fauna associated with lagoons, e.g. Gasterosteus aculeatus, Idotea viridis, etc. C. glaucum occurs throughout the majority of the length, especially in the middle section, and abundantly in places. The salinity was 17.3‰ (S.G. 1.0135

at 15.75°C.) measured on the 28th August 1968. On the 20th March 1969 the salinity was recorded as 10.4‰ (1.85 x 10^5 C.U.'s) and as 16.0‰ (2.5 x 10^5 C.U.'s) on the 17th June 1969. For these latter two values, I am indebted to H.J.G. Dartnall. Therefore, it appears that salinity is reasonably constant, though it appears from local knowledge (communicated by H.J.G. Dartnall) that the lagoon is 'topped up' through a sluice during spring tides. The substratum is very soft and anaerobic, and the cockles are never exposed to aerial conditions.

The Isle of Sheppey was investigated thoroughly as was the rest of the Kent coast, but no other marine lagoons were discovered.

(v) Sussex

(a) Cuckmere Haven. (O.S. map 183. Grid ref. 516.990)

For information concerning this locality I am indebted to Miss J. Chatfield. At Cuckmere Haven, the Cuckmere river enters the sea. Here a new straight drainage channel has been cut for the river, leaving near the mouth, a double 'S'-shaped brackish water lagoon, resembling an ox-bow lake, which was the old river course. This lagoon is isolated from the sea by a shingle ridge, and from the new river channel by banking. It received fresh water drainage at its northern end, and presumably salt water seeps into the lagoon at its southern portion and/or enters the lagoon on occasions of flood or spring tide from the new river cut. Large, healthy C. glaucum occur in dense numbers locally in this lagoon and the periostracum of these individuals is particularly extensively developed. They occur in soft mud and are permanently submerged. The associated fauna appears to be more sparse than in other marine lagoons, with only Idotea viridis and Carcinus maenas as obvious members. Chaetomorpha crassa occurs in dense patches.

The water salinity varies, increasing towards the sea-ward end of the lagoon. On the 14th March 1968 the salinity was recorded as 3.75‰ (S.G. 1.0035 at 7.5°C.) at the northern part, increasing to 10.75‰ (S.G. 1.0095 at 7.5°C.) in the middle section, where C. glaucum is common. On the 12th May 1968 the salinity was 7.5‰ and 20.3‰ at the two respective stations, and on the 12th April 1969 the salinity at the latter station was found to be 17‰ (2.5 x 10^4 C.U.'s). The salinity of this pool is therefore very variable, and it appears that both fresh water and sea water enter the pool during the year.

(b) Widewater, Shoreham-on-Sea. (O.S. map 182. Grid. ref. 201.042)

This lagoon is separated from the sea by a shingle ridge and appears to maintain a relatively stable high salinity. It is non-tidal and is probably a seepage pool. The bottom is shingle, covered by fine mud. Ellis (1932) recorded that C. edule var lamarcki (Reeve) and C. edule var gudrata (Bucquoy) occurred in the lagoon. C. glaucum was the only cockle discovered to be present.

For the communication of this site I am indebted to P.J. Russell, who has conducted a survey of the environmental parameters of the lagoon (see Russell, 1969). On the 14th March 1968 a salinity of 19.8‰ (S.G. of 1.0165 at 7.5°C.) was recorded. By the 12th May 1968 the salinity had increased to 22.2‰ whilst on the 21st April 1969 the salinity was 26‰. In the summer of 1970 a salinity of 38‰ was recorded for this locality.

The fauna associated with C. glaucum is noted by Ellis (1932) and includes Littorina saxatilis, Idotea viridis, and Gasterosteus aculeatus.

Chaetomorpha crassa is extremely abundant in this lagoon and the cockles are permanently submerged.

(c) Pagham. (O.S. map 181. Grid refs. between 878.965 and 883.966)

Tebble (1966) records Cerastoderma glaucum (as Cerastoderma lamarcki) from Pagham, Sussex. Pagham harbour contained a small population of C. edule. This region is tidal and estuarine in nature. However, in the sides of drainage channels, of this tidal mud flat, can be found thin dead shells of C. glaucum, apparently occurring in living assemblages. This indicates that at one time this location was probably a lagoon.

Two lagoons lie adjacent to the harbour entrance. The smallest, which was dried out in the summer of 1968, did not contain any live C. glaucum, whilst in the second was discovered only a few live individuals. This lagoon also contains numerous isopods (Sphaeroma species) and small Mya arenaria. A fine layer of mud covers the shingle base of the pool. A wide shingle ridge separates this pool from the sea, but sea water may enter from the harbour entrance via the small lagoon on occasions of flood spring tides.

(vi) Hampshire

(a) Hermitage swimming pool, Portsmouth. (O.S. map 181. Grid ref. 748.054)

This pool contained numerous C. glaucum in the spring of 1968. The salinity was low 8.5‰ (S.G. 1.007 at 14.5°C.) on the 12th May 1968, and had increased to 10.4‰ on the 6th June 1969. A thick, soft mud covers a shingle base and fresh water drains into the pool from the land. A concrete wall prevents access by the sea during normal tides but a sluice gate is presumably used to renew the water periodically. An examination in the autumn of 1969 yielded no live C. glaucum, and local knowledge showed that in fact the pool has been drained for repair to the sluice gates. Whether any of the original C. glaucum population survived

is not known. The cockles collected in 1968 appeared to be in poor condition, being 'watery' in appearance. This may well have been due to collection immediately after spawning, or to the low salinity of the environment. The associated fauna in 1968 included Gasterosteus aculeatus, Gobbius minutus, Idotea viridis, Carcinus maenas and Arbra sp.

In 1968 several C. glaucum were discovered on the foreshore in the stream of brackish water running from the sluice gates. These individuals were effectively covered by water for the majority of the low tide period, and thus are not truly intertidal in the accepted sense, as they are seldom exposed to air.

(b) Horsey Island lake. (O.S. map 180. Grid ref. 635.043)

Russell (personal communication) informed me of this locality in Portsmouth Harbour. Horsey Island is the northern-most island within the Harbour. It contains a deep (c. 10 meters) artificial lake used by the Royal Navy for diving training. Access to the sea is afforded via lock gates, but they only seem to be used infrequently to maintain the water level. The diving school of H.M.S. Vernon was kind enough to collect a sample of C. glaucum from the lake bottom on the 14th March 1968. The salinity of surface water was 24.2‰ (S.G. = 1.0195 at temp. of 10.9°C.). A fine weed, probably Chaetomorpha covers the lake bottom.

The cockles are therefore permanently submerged in a non-tidal lake living within fine mud.

(c) Alverstoke golf course lagoon, Gilkicker Point, Gosport. (O.S. map 180. Grid ref. 608.978)

This tideless lagoon is separated from the sea by a sea wall, but a sluice pipe does allow connection to the sea, presumably as a flood protection device. Normally this pipe is not in operation, and the lagoon is effectively isolated.

The pool is shallow (maximum depth probably c. 2 meters) and contains masses of Ruppia maritima and Chaetomorpha crassa. It is stony around the northern edges, but overlain by fine mud a few meters from the edge. Within this substratum are found relatively large, quite thick shelled, C. glaucum. These individuals have particularly white shells and are extensively covered on the outer surface by periostracum. The associated fauna includes Gasterosteus aculeatus, Arenicola marina, Idotea viridis, Hydrobia ventrosa, Lepidochitona cinereus, Diadumene cincta and Botryllus schlosseri.

This lagoon was examined on the 6th June 1969 and a salinity of 28.2‰ (10^5 x 3.9) was recorded. The temperature of the water varied from 18.75°C. at the edge to 14.5°C. at a depth of 40 cms. The air temperature in the sun was 19.0°C. This indicates that large temperature fluctuations do occur in these lagoon localities. Although temperature stratification probably occurs, the rapid attainment of high water temperatures has most important implications on, for example, the physiology of breeding in lagoonal populations of C. glaucum.

(d) Lymington (Hampshire).

The Salterns, Near Woodside, Lymington. (O.S. map 180. Grid ref. 328.939)

This marine pool used for yachting, is filled via a sluice. From local knowledge it seems that the deepest parts of the lake remain even when the rest of the pool is drained. Many dead shells (spat in weeds and adults) were discovered, but the deepest sections of the pool where live cockles would be expected, could not be reached from the shore. It is interesting that one old C. glaucum shell, found, had winter growth disturbance rings normally associated with cockles living in littoral locations.

(vii) Isle of Wight

A study of the Ordinance Survey map of the Isle of Wight indicated the existence of several pools, which appeared to be likely locations of C. glaucum populations. In the summer of 1969 Mr. D. Lane kindly visited one of these localities at Hills Dam, Brading Harbour. Several pools are retained here at low tide, and dead shells of C. glaucum were discovered in one of these pools. It is likely that other localities such as the boating pool at Sandown, Newtown Bay Pool, Yarmouth Pool, and lagoons at Ryde could yield live C. glaucum.

(viii) Dorset

(a) The Fleet, Weymouth. (O.S. map 178. Grid refs. 666.762 to 569.840)

This locality which approximates more to a loch or a fjord than a true lagoon, stretches for approximately 8 miles from Weymouth Bay to Abbotsbury to the north-west. It grades from purely marine conditions at its mouth between Portland and Dorset mainland, to brackish and then almost to fresh water, at Abbotsbury. Russell (personal communication) reported the presence of C. glaucum in this stretch of water, and has conducted a thorough survey of this site, (see Russell, 1969).

Exceptionally large C. edule were discovered living in the sand of the Weymouth section of the Fleet. This region is tidal and typically littoral. The fauna associated with these cockles are those found on intertidal flats including Mya arenaria, Scrobicularia plana, Macoma balthica, Arenicola marina, Carcinus maenas, Corophium vulutator.

At Wyke Regis the Fleet narrows sharply, before broadening out into an extensive mud-bank system. These banks are covered by Zostera sp. and Enteromorpha intestinalis which dam the water, preventing complete loss of water from the upper Fleet. On the narrow shore which occurs in this region, small globular, stunted C. glaucum were found. These were

~~shown~~ proven to be C. glaucum and not C. edule by the presence of a black digestive gland, which has been shown to be of diagnostic value in the separation of the British Cerastoderma, (Boyden, 1969). The shells of these cockles were of a yellowish hue and morphologically were attributable to C. glaucum by the presence of a short ligament. They were found intertidally often covered by Enteromorpha. However, exposure to air was only for a short period, probably for a maximum of 2 - 3 hours per tide, and the cockles were protected from desiccation by the Enteromorpha. However, by their apparently stunted appearance, and with reference to their symbiont fauna (see section VII) it seems that these cockles were in poor condition.

At Langton Heering the water drops only a matter of a few centimeters at low tide, and therefore cockles in this region were permanently submerged. Here C. glaucum abounds, and an extensive population of this cockle occurs within soft mud amongst the roots of the Zostera. The salinity of this region on the 12th August 1968 was recorded as 29.20‰ (S.G. 1.0215 at 21.25°C.).

The Fleet is, therefore, a region of gradation from true littoral to lagoon pool conditions, and parallels very much the conditions found in Danish fjords (Høpper-Petersen, 1958; Russell, 1969). The type of cockle present changes from C. edule at the Fleet mouth, to C. glaucum in the lagoonal region. Stunted C. glaucum occur where lagoon conditions are not complete, on the narrow shore of the middle fleet. Russell records C. edule along the deepest channel between the mud banks of the middle Fleet, where tidal flow is strongest, but it is absent elsewhere in the mud bank region. Therefore, it appears that the conditions of the middle Fleet are not suitable for the occurence of a mixed population of the two cockles. It would seem that the two cockles are only found

where their own requirements, of permanent submersion for C. glaucum and tidal flow for C. edule, are met by the environment.

(b) Poole harbour area (O.S. map 179. Grid ref. 045.885)

Poole harbour and the surrounding coastland was visited during May 1970. No lagoon populations of C. glaucum were found in this area. However, a sample of cockles collected from Sandbanks, near the entrance to the harbour was found to contain 23 C. edule and 8 C. glaucum. It would seem very likely, therefore, that quite extensive populations of C. glaucum occur in the innermost regions of this harbour.

2. Fieldwork to determine the distribution of Cerastoderma glaucum (Poiret) elsewhere in the British Isles

C. glaucum has, therefore, been found around the south-east coast of England from North Norfolk to Dorset. From a study of Ordinance Survey maps it can be seen that to the north of Norfolk the number of suitable pools for colonisation by C. glaucum is very low. Hence, it is not surprising that this cockle has not been recorded north of Wells-next-the-sea, Norfolk, along the English north east coast, by the Conchological Society Marine Census. Similarly, there are no authenticated recordings of populations of C. glaucum to the west of the Fleet, Weymouth, Dorset. Thus for geological reasons few or no lagoons occur in north-east England or around south-west England. It was noted, however, that pools did occur along the South Wales coast and in south-east Ireland. A field study of these areas was conducted in the summer of 1969 to determine if C. glaucum occurred in these regions or whether its distribution was limited solely to south-east England.

a. South Wales

Several pools occur along the coast between Haverford West and Cardiff. However, only one at Rhoose Lousse, near Barry (O.S. map 154. Grid ref. 036.662) was discovered to be marine. This pool was separated from the sea by a sea-wall and probably has a maximum depth of 3-4 feet. A small brackish stream runs in from the east, whilst to the west it is bordered by the Aberthaw Power Station. Fly-ash from the Power Station threatens the continued existence of this lagoon. The substratum varies from very muddy to rocky, large boulders occurring on the sea-ward and eastern flanks of the lagoon.

In the muddy regions abundant weed growths of Ruppia maritima and Chaetomorpha crassa occur. Within the strands of this latter alga were discovered small spat of C. glaucum, whilst larger individuals occurred in the mud. Many dead shells of C. glaucum were also found around the lagoon edges, together with valves of old Macoma balthica and Scrobicularia plana. The associated fauna was typical of marine lagoons e.g. Gasterosteus aculeatus, Palaemonetes varians, Hydrobia ventrosa, Idotea sp. Chironomid larvae also occurred within the mud.

At the time of examination on the 30th July 1969 the specific gravity measured = 1.01475 at 24.25°C., giving a salinity of 21.4‰.

This site was, therefore, of non-tidal, lagoonal nature, containing a permanently submerged population of C. glaucum. The juvenile cockles occurred in Chaetomorpha crassa, whilst the adults were found within the soft mud substratum.

b. Field study of south-eastern Eire

Two sites at Ferrybank, Arklow, (½" to 1 mile O.S. sheet 19. Grid ref. 25.74) and at Lady's Island Lake, Wexford (O.S. sheet 23. Grid ref. 10.05) are seemingly normal saline lagoons. The former contained abundant Chaetomorpha crassa and other fauna typically associated with seepage pools. However, neither locality contained C. glaucum populations. Black strand (O.S. sheet 23. Grid ref. 62.02), Tacumshin lake (O.S. sheet 23. Grid ref. 05.06) and Broad lough (O.S. sheet 16, grid ref. 31.95) were localities where it was thought possible that mixed cockle populations ~~of the two cockles~~ could have occurred. They are lochs having a narrow connection with the outside sea, the former two draining at time of low tide. Zostera occurred in both of these two strands, but C. edule was the only cockle present. However, during collection of C. edule from Wexford harbour at Burrow, Rosslare (O.S. sheet 23,

grid ref. 09.16) dead shells were collected and found to be C. glaucum. These valves were old, usually separate, but indicate that, at least at some time, C. glaucum did occur in this region, although no living population of this cockle was discovered.

Thus, in this survey, living populations of C. glaucum were not discovered south of Dublin or east of Cork in Eire.

c. Field study of western and south-western Eire

Forbes and Hanley (1853) record C. glaucum from the Great Aran Islands in Galway Bay. They describe these cockles as occuming suspended in weed, and this alone gave credulity to what appeared at first glance to be an unlikely location of a C. glaucum population.

In the summer of 1969, lagoons south of Galway near Kinvarra were examined for cockles. Two living populations of C. glaucum and a locality where only dead shells occurred were discovered.

(1) Trawnagh, Kinvarra Bay. (Bartholomew ½" map 5, 8°59' W. 53°10' N.)

This lagoon is separated from Kinvarra Bay by a narrow spit of land bearing a minor road. A pipe drains from the pool into the bay, but water is retained in the lagoon at low tide. Chaetomorpha crassa abounds with Ulva lactuca at the pool sides. Examples of the associated fauna are Gammarus sp., Idotea viridis, Littoria littorea, Arenicola marina, Gasterasteus aculeatus, Gobbius minutus and Palaemonetes varians.

C. glaucum occurs abundantly, suspended in Chaetomorpha or in the very soft, silt substratum. On the date of examination, 4th August 1969 the S.G. = 1.0195 at 19.5°C., giving a salinity of 26.25‰.

Effectively the cockles were permanently submerged, and although connection between the lagoon and the sea was possible through a narrow pipe; the site resembles a seepage pool.

(ii) Finavarra (Map 5. 9°9' W. 53°9.5' N.)

This locality is a completely land locked lagoon, choked with Chaetomorpha crassa and some Ruppia maritima. C. glaucum collected were small (up to 20 mms. in length) and were mainly suspended within the weed. The population number did not appear to be very large, neither were the cockles very large. They also appeared ~~also~~ to be in poor condition. The shells were brittle and completely white internally, with the absence of any purple or brown staining on the inner surface of the shell valves.

On the 4th August 1969 the S.G. was 1.006 at 20.5°C. giving a salinity of 8.7‰ whilst on the 11th August 1970 the salinity recorded was 9.5‰. This was one of the lowest salinity environments where living C. glaucum have been found to occur in a lagoon, and judging by the poor condition of these cockles the locality could reflect a population being eliminated by gradual salinity reduction.

(iii) Aughinish, Galway Bay (Map 5, 9°5' W. 53°10.5' N.)

This locality represents a pool which is replenished at high spring tides. According to local information the pool almost dried out during June 1969 but was replenished by August. A nucleus of cockles probably survive in the deepest parts of the lagoon. Dead shells, from spat size to large specimens (40.50 mm. length), were found at the pool edges. Other shells of marine origin also occurred, and were probably swept into the pool at spring tides. This would appear to be a natural seepage pool locality, filled at spring tides.

Thus, the presence of C. glaucum in the Galway Bay area was confirmed. By examination of the Ordinance Survey maps of Connemara it seemed highly likely that many other populations of this cockle could

also occur in this region, as lagoons or seepage pools appeared to be especially common between Galway and Westport. This region of coast was visited during the summer of 1970 and several living populations of C. glaucum were discovered.

(iv) Salt Lake (loch), Clifden, Connemara, Co. Galway (Map 5. 10°2' W. 53°28' N.)

This large loch has a narrow entrance to the outside sea, and water is retained in large volume at low tide. In fact, in the upper regions the tidal rise and fall is only a few centimetres. The substratum is composed mainly of small, weed covered boulders, but between these rocks are areas of fine gravel and mud. In these regions both C. edule and C. glaucum occur together, even in the middle reaches of the loch where tidal movement would appear to be small. The presence of C. edule in such a lagoonal type habitat seems to be in contrast to other localities. It is noted, however, that this loch is very large and the extent of the cockle population is relatively small because of the rocky substratum. Water movement owing to wind and tidal action is probably quite considerable in this large exposed loch.

On the 9th August 1970, the salinity was 31.25‰ at the narrow entrance to the sea, lowering to 28.75‰ about one mile from the entrance. Both cockle types exhibited annual growth rings upon the shell although aerial exposure may only briefly occur in those individuals near the loch entrance.

This population was the farthest north that living C. glaucum were discovered in Eire. Other localities north of this site up to Newport, Co. Mayo were examined, but no living C. glaucum were located. A list of these sites, together with other localities examined during the 1969 and 1970 surveys can be found in Appendix III.

(v) Curhownagh loch between Drimmeen and Maum (Map 5. 10°4' W. 53°27' N.)

This small sea loch, situated about four miles west of Salt Lake also contained a population of C. glaucum. The tidal rise and fall of this loch was very small, and C. edule was not discovered within the confines of the loch.

(vi) Unmarked lagoon south-east of L. Anaserd (Mannin Peninsula) - near Ballyconneely Bay (Map 5. 10°4' W. 53°24' N.)

At this locality C. glaucum were found within the very soft mud which covered the lagoon bottom. The salinity of this pool was recorded as 23.3‰ on the 10th August 1970. This population occurred in lagoon conditions and were never exposed to air. C. edule was absent.

(viii Loch at Keeraunnagark, Cashla Bay, North Galway Bay (Map 5. 9°34' W. 53°14' N.)

This shallow tidal loch contained a population of large C. glaucum within the soft substratum. These cockles were, however, never or very rarely exposed to air and were thus within a lagoonal type habitat. The salinity was recorded as 31.8‰ on the 11th August, 1970.

(viii) Chapeltown, near Tralee, Kerry (Bartholomew Map 4. 9°51' W. - 52°10' N.)

This locality resembles a loch, being a pool joined to the sea via a narrow entrance. At low tide the loch drained almost entirely but some water is retained in rivulets on the mud flat. Zostera sp. is abundant, and Pelvetia canaliculata, Fucus spiralis and Ulva lactuca occur on boulders on the upper shore. The associated fauna is of the typical littoral type, e.g. Arenicola marina, Littorina saxatilis, L. littorea, Macoma balthica etc.

Cerastoderma edule occurred throughout the loch, the largest specimens occurring near the entrance to the sea and in the main deeper channels. Stunted, globular individuals occurred amongst a few large C. glaucum, whilst in parts of the 'pool,' where water only covers the cockles for approximately 3-4 hours in every tide, only stunted C. edule occur. C. glaucum ranged from very small spat to fairly large adults in the soft mud. Here water was only slowly drained at low tide, and protection from desiccation was afforded by the dense Zostera beds. The population of this cockle was not very extensive.

On the 7th August 1969 when this locality was studied, the salinity was identical outside the loch entrance and at stations within the loch . The S.G. = 1.0255 at 16.25°C. giving a salinity of 33.2‰. When visited on the 14th August 1970, the salinity was recorded as 34.7‰ in the innermost regions of the loch.

(ix) Unmarked saline loch at Rosscarbery, Southern Cork. (Map 4 9°2' W. - 51°39' N.)

This loch again had a very narrow entrance to the sea, but water is retained so that the cockles found within the sandy-mud substratum are never exposed to air. The tidal rise and fall is low and the loch appears to be quite deep in places. The salinity of the loch was recorded as 29.7‰ on the 24th August 1970.

C. edule occurred on the foreshore of the adjacent marine bay, but no live C. edule were found in the loch although dead shells of this cockle were discovered within the loch confines.

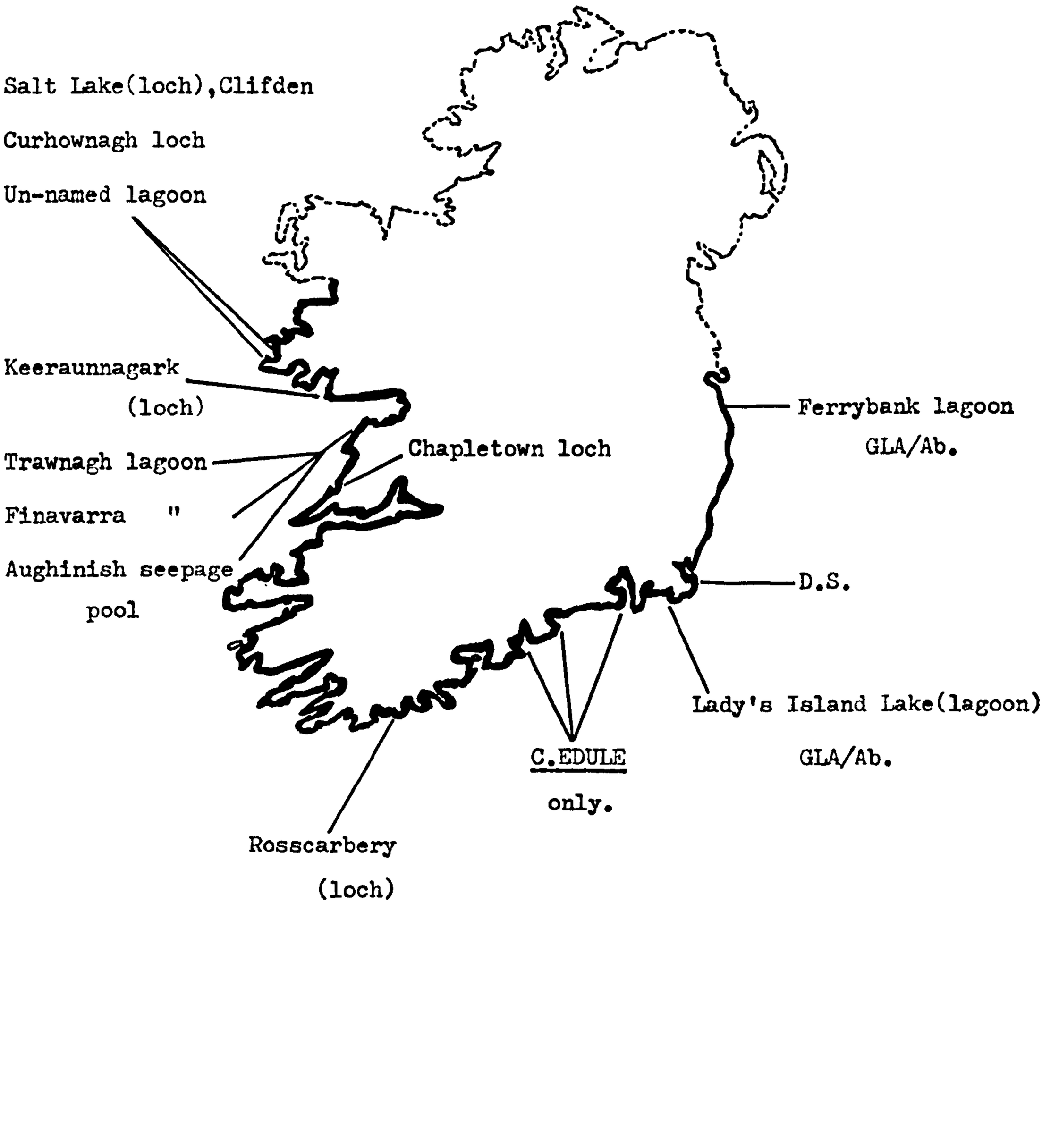
This locality was the most southerly and eastern site in Ireland where a living population of C. glaucum was discovered. The distribution of C. glaucum in Ireland has been summarised in figure 2.

Fig 2 - Distribution of Cerastoderma glaucum in Eire.

———— = Coastline surveyed

– – – – – = Unsurveyed coasts

GLA/Ab. = Lagoon localities where C.glaucum was absent



d. Discussion of Field Investigations

(i) Salinity Tolerances

Isolated salinity measurements of lagoon sites of C. glaucum populations cannot be used critically to indicate the true or overall salinity that is affecting the cockles. Howes (1939) studying New England Creek, Essex in 1934-5 showed a salinity variation over a year of 6.4‰ (21.5‰ to 27.9‰). Similarly, Russell (1969) showed a variation of 9.6‰ (22.8‰ to 32.4‰) at Widewater, Sussex. Other localities such as Cuckmere Haven Lagoon, Sussex, show considerably larger salinity variations, even in surface water collected at the same time, from different positions around the pool. Salinity stratification can also occur with fresh water overlying saline water. Even so, although the salinity measurements are inherently unreliable, some indication of the general salinity range of the lagoon sites containing living populations of C. glaucum can be obtained. This information is recorded in table 2.

From table 2 it can be seen that the minimum salinities from which live C. glaucum have been collected are 8.5‰ from Hermitage swimming pool and 8.7‰- 9.5‰ from Finavarra, Eire. The condition of the cockles from both of these sites appeared to be rather poor. The Irish locality is well isolated from the sea and seems to be experiencing a gradual reduction of salinity, and therefore the salinity measurement was probably reliable as regards to indicating the 'true' salinity of the environment. It would, therefore, seem that c.8.5‰ is the minimum salinity in which C. glaucum can survive. Hopner-Petersen (1958) records that C. glaucum occurs down to 5‰ but because of the fjord nature of the Danish sites, he investigated, it is probable that this salinity was not maintained at this value throughout the year. The salinity of lagoons

Table 2

Salinity recordings from various lagoons containing populations of Cerastoderma glaucum (Poiret)

Locality	Date	Salinity	Salinity range	General comments	Authority
Holkam Gap, Norfolk	10. 2.68	20.9 ‰		Very large individuals	Russell(1969)
Wells-next-the-sea, Norfolk	10. 2.68		(13.3-17.5 ‰)		" "
Shingle Street, Suffolk					
Lagoon 4	(1966-7)		(28.5-31.7 ‰)	small population	" "
Lagoon 7	"		(29.7-34.6 ‰)	" "	" "
Brightlingsea, Essex	7. 5.68	20.3 ‰		" individuals	
	27.12.68	23.4 ‰			
New England Creek, Essex					
Large lagoon	(1934-5)		(21.5-27.8 ‰)		Howes(1939)
	28. 1.68	21.6 ‰			
small lagoon	"	18.5 ‰		large, thriving population	
lagoon ajacent to Shelford Creek	"	17.0 ‰			
Sheerness, Kent	28. 8.68	17.3 ‰		large number of small	
	20. 3.69	10.4 ‰		individuals	
	17. 6.69	16.0 ‰			
Cuckmere Haven, Sussex	14. 3.68	10.8 ‰		cockles abundant	
	12. 5.68	20.3 ‰			
	12. 4.69	17.0 ‰			
Widewater, Shoreham, Sussex	(1966-7)		(22.8-32.4 ‰)		Russell(1969)
	14. 3.68	19.8 ‰			
	12. 5.68	22.2 ‰			
	21. 4.69	26.0 ‰			

Table 2 - continued

Locality	Date	Salinity	Salinity range	General comments	Authority
Pagham	(1966)	15.5 ‰			Russell(1969)
Hermitage, Portsmouth	12. 5.68.	8.5 ‰		condition of cockles poor, none collected in 1969	
	6. 6.69.	10.4 ‰			
Horsey Island Lake	(1966)	27.0 ‰			Russell(1969)
	14. 3.68.	24.2 ‰			
Alverstoke, Gosport	6. 6.69	28.2 ‰		large individuals	
The Fleet, Dorset	(1966)		(8.8-33.8 ‰)		Russell(1969)
	12. 8.68.	26.7 ‰			
Rousse, Nr. Barry, S.Wales	30. 7.69.	21.4 ‰			
Travanagh, Kinvarra, Eire	4. 8.69.	26.2 ‰			
Finavarra, Eire	4. 8.69.	8.7 ‰		cockles watery in appearance,	
	11. 8.70.	9.5 ‰		some dying	
Ballyconneely lagoon	10. 8.70.	23.3 ‰			
Keeraunnagark loch	11. 8.70	31.8 ‰		not true lagoon	
Rosscarbery loch	24. 8.70	29.7 ‰		" " "	

is probably more accurate in measuring the minimum salinity tolerance of C. glaucum. Høpner-Petersen also records C. glaucum as breeding in 10‰ in Dybsø fjord, Denmark, thus the minimum salinity for survival of populations of C. glaucum is probably between 8.5 and 10‰. This minimum salinity may well indicate an ecological barrier within brackish waters. Vălikangas (1933), considering brackish waters in the North Sea - Baltic area, divides brackish waters, as regards to salinity, in the following manner:

		S‰
Brackish water	Oligohaline	(0.2 - 0.5) - (2 - 3)
	Meiomesohaline	(2 - 3) - (8 - 10)
	Mesohaline	
	Pleiomesohaline	(8 - 10) - 16.5
	Polyhaline	16.5 - 30
Marine water		30

Evidence from the survival of C. glaucum in low saline environments would support the division of mesohaline brackish water at 8 - 10‰. Remane (1934, 1940) suggested a slightly different terminology to Vălikangas, but retained a border at 8 - 10‰ as is shown below:

	S‰
Typical brackish zone	5 - (8 - 10)
Brackish - marine transitional zone	(8 - 10) - (15 - 16.5)
Marine water	(15 - 16.5)

Ekman (1953), however, is more dogmatic, placing a border at 10‰.

	S‰
Mesohaline brackish water	3 - 10
Polyhaline brackish water	10 - (17 - 20)
Oligohaline sea water	(17 - 20) - 30
Meohaline sea water	30 - 34

A criticism of the above terminology can be found in Dahl (1956) who supports the original divisions of Välikangas. It is interesting that conclusions from salinity measurements of lagoons in the British Isles cited here, and previous work in the North Sea - Baltic region, are similar, and support the validity of the ecological delimination of zones within brackish waters in the region of 8 - 10‰.

The overall range of salinity of lagoons in the British Isles recorded by the author is from 28.2‰ to 8.5‰. Oceanic sea water gives a salinity of c.33 - 36‰, and therefore the lagoon sites around Britain can all be regarded as brackish water localities. However, the C. glaucum found in the mixed populations of Chapeltown, Kerry, and Salt Lake, Galway in Eire are bathed by higher salinity waters: 33.2‰ and 31.25‰ respectively. Also, as C. glaucum is recorded as occurring in the Mediterranean, (Mars, 1951; Russell, 1969), where salinities higher than 36‰ are found, this cockle seems to be able to tolerate a greater salinity range than C. edule. In estuaries, wide salinity fluctuations occur, and these are typically the habitat of C. edule. However, prolonged periods of large salinity reduction are rare, and thus meaningful values of salinity tolerances of C. edule are difficult to determine. Høpner-Petersen (1958) does not record C. edule in waters of salinity below 20 - 25‰. For further comments concerning salinity tolerances of the Cerastoderma, see Section V - 3(g).

(ii) Conclusions on ecology and theories concerning distribution of C. glaucum

C. edule is widely distributed around the British Isles coasts, (See map 1, section III) and is found typically in littoral conditions. It is a prominent member of mud flats and estuarine fauna, but occasionally occurs sub-littorally. C. glaucum on the other hand is generally found permanently submerged in land-locked marine pools. The qualities of a 'glaucum' site appear to be simply a stagnant saline lagoon, isolated from tidal influences, (Boyden, 1969). However, between these two extremes of typical environments are a few localities, that are intermediate in qualities and where mixed populations occur e.g. The Roach and Crouch estuaries, Horsey Island foreshore, Hermitage foreshore, The Fleet, Poole harbour, Chapeltown loch and Salt Lake, Eire. Each locality has been described and compared to the typical habitat for each cockle type. From the analysis of these sites the factors which appear to be essential as regards the environmental requirements of each cockle are:

(1) C. glaucum - Permanent or near permanent submersion in stagnant, saline pools or on the shore in very sheltered conditions.

(2) C. edule - Littoral locations, or regions where some water movement occurs.

The fact that mixed populations do not commonly occur indicates the separation between the two cockles in habitat preference, and the degree of divergence which has occurred between the two forms.

It is interesting at this stage to examine the European distribution of the two cockles. C. edule extends southwards along the Atlantic coasts of France and Spain to North Africa, (Ekman, 1953), and northwards to the Netherlands, Danish and Norwegian North Sea and Atlantic coasts.

(Ocklemann, 1958; Høpner-Petersen, 1968). It is also found in the approaches to the Baltic where oceanic effects are still evident, e.g. the Kaltegat shores of Sweden and Denmark (Høpner-Petersen, 1968, written communication; Russell, 1969). C. glaucum, on the other hand, is found in the Baltic and in the inner portions of Danish fjords removed from the effects of saline Kattegat water (Høpner-Petersen, 1958; Russell, 1969). C. glaucum is also found on the French Mediterranean coasts, (Mars, 1951), and the Algerian Mediterranean coast (Poiret, 1789). Russell (1969) is of the opinion that C. glaucum is the only Cerastoderma occurring in the Mediterranean, and this is supported by observations by the author on collections of Mediterranean Cerastoderma in the British Museum (Natural History section). Both the Baltic and the Mediterranean have a very small tidal rise and fall, thus the cockles remain permanently submerged in basically still or slowly changed water. The lagoon 'glaucum' sites occurring in southern England can be considered as miniature versions of these non-tidal seas, (Boyden, 1969).

Around the British coasts C. glaucum is found in pools where the salinity is usually a little, or considerably lower, than oceanic water. Nevertheless, this character of the lagoons may not be the essential demand dictating the occurrence of C. glaucum. Continual submersion in stagnant, saline water appears to be the primary requirement or habitat essential demanded by this member of the Cerastoderma.

Morphologically C. edule is very variable and some thiry-five varieties have been described (Mars, 1951; Grossu, 1961). Even around the British shores, C. edule collected from different localities can often be recognised by their local shell characteristics. Thus, Southend cockles can be separated from those of the estuarine River Crouch, and

Weymouth, Scilly Isles, South Wales and Anglesey cockles are also identifiable by their shell shape. However, all these cockles fall into the category of C. edule. Therefore, C. edule is a very variable species as regards shell shape and around the British coasts there are many 'ecotypic' varieties, which should not be confused with specific types. Thus, typically there is not a range from 'edule' type to 'glaucum' type on the shore, the occurrence of C. glaucum in pools seems to be independent of the presence of C. edule on the adjacent foreshore. Occasionally isolated C. glaucum individuals have been collected from the shore (see earlier), but their presence can often be explained by reference to escape from near-by lagoon populations. Around the majority of British shores, C. glaucum is confined to lagoons and littoral populations are exceptions, not the rule. Thus, it would be difficult to imagine that the distribution of C. glaucum is determined by larvae released from the occasional specimen of this cockle found on the shore.

How can the distribution of C. glaucum in south east England be exphined? It occurs in widely apparated isolated localities and there appears to be no relationship between one site and another. If dispersion of the species relies upon the larval stage, then distribution would be extremely fortuitous and dependent upon chance removal from pools. In the sea the larvae could be dispersed by tidal currents, and then finally re-introduced into another suitable lagoon locality. Such a method would seem to be extremely hazardous. However, if C. glaucum is shown to have a long larval life before settlement occurs, then this mode of dispersion may be feasible.

Boyden (1969) is of the opinion that the modern distribution of C. glaucum in south-east England reflects a much wider distribution in

Fig 3 -

GEOLOGICAL MAP OF SOUTH-EAST ENGLAND
INDICATING THE DISTRIBUTION OF ALLUVIAL DEPOSITS

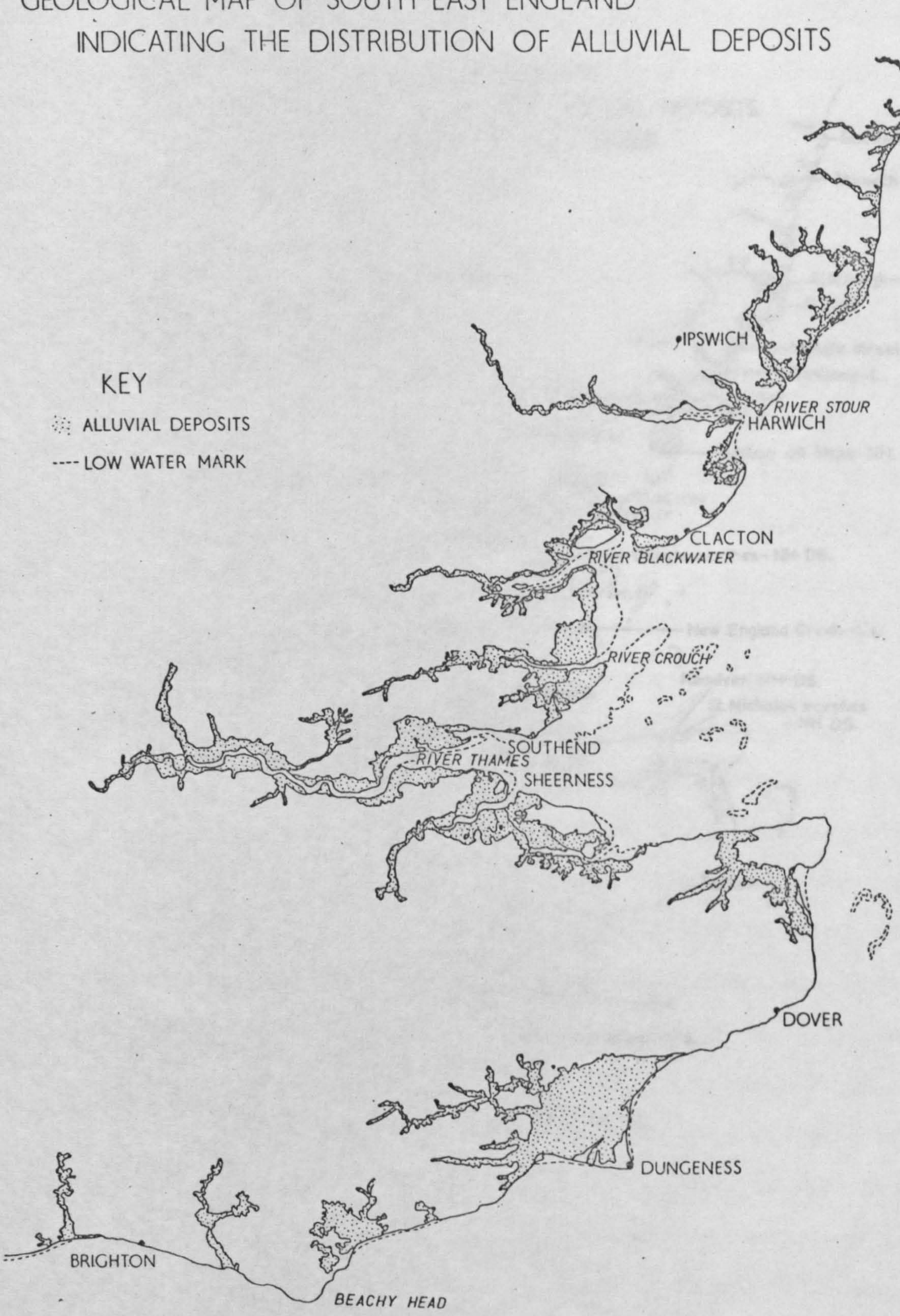
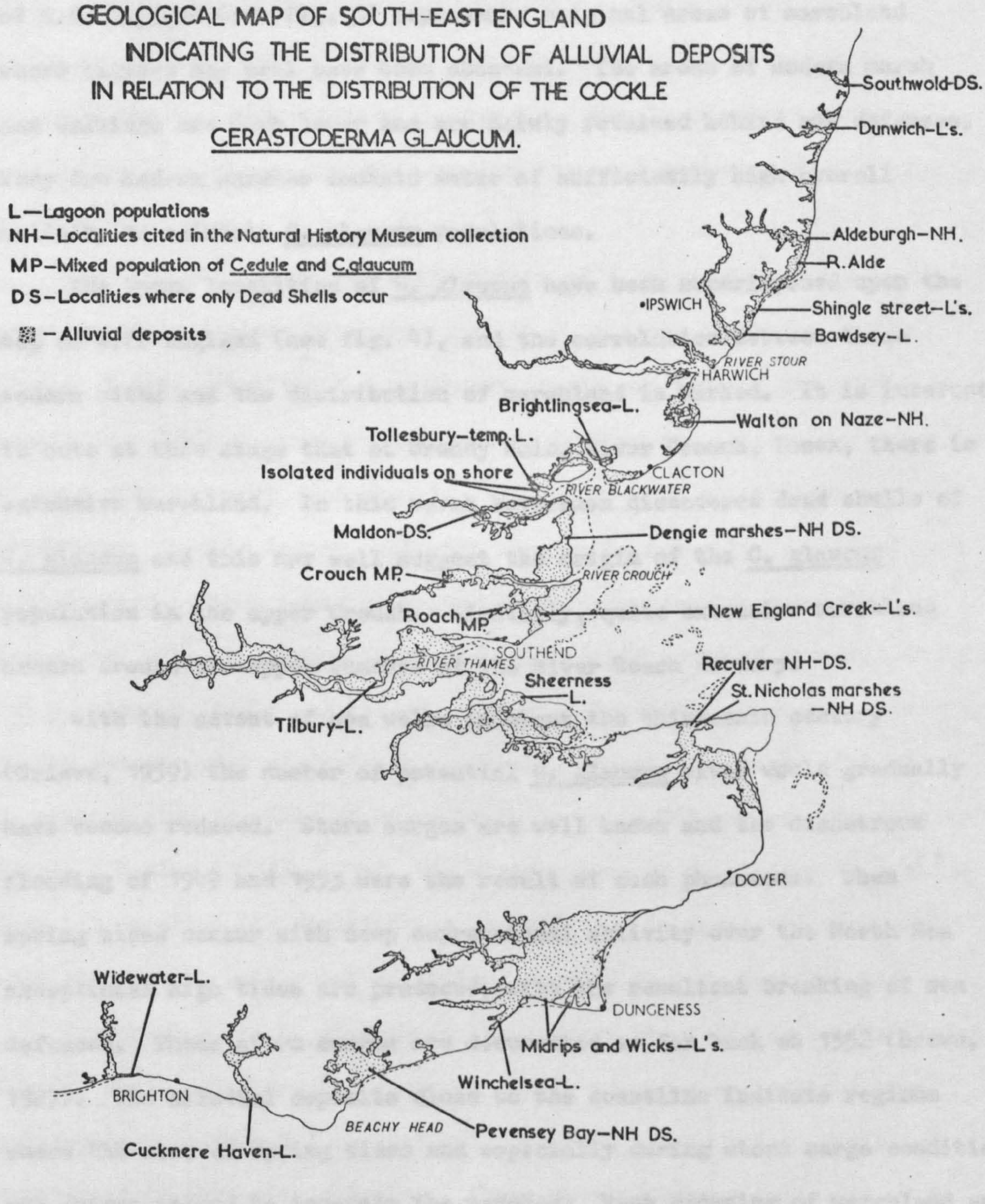


Fig 4 -

GEOLOGICAL MAP OF SOUTH-EAST ENGLAND
INDICATING THE DISTRIBUTION OF ALLUVIAL DEPOSITS
IN RELATION TO THE DISTRIBUTION OF THE COCKLE
CERASTODERMA GLAUCUM.



previous times. It is argued that in recent geological times, saline or brackish water lagoons were probably much more common than they are at the present day. The region of alluvium shown in the geological map of S.E. England (see fig. 3) represents original areas of marshland where lagoons may well have been abundant. The areas of modern marsh and saltings are much lower and are mainly retained behind sea defences. Very few modern marshes contain water of sufficiently high overall salinity to maintain C. glaucum populations.

The known localities of C. glaucum have been superimposed upon the map of S.E. England (see fig. 4), and the correlation between these modern sites and the distribution of marshland is marked. It is interesting to note at this stage that at Brandy Hole, River Crouch, Essex, there is extensive marshland. In this marsh have been discovered dead shells of C. glaucum and this may well suggest the origin of the C. glaucum population in the upper Crouch. Similarly, quite extensive marshland occurs around the upper reaches of the River Roach estuary.

With the advent of sea walls in about the thirteenth century (Grieve, 1959) the number of potential C. glaucum sites would gradually have become reduced. Storm surges are well known and the disastrous flooding of 1949 and 1953 were the result of such phenomena. When spring tides concur with deep depressional activity over the North Sea exceptional high tides are produced, with the resultant breaking of sea defences. These storm surges are documented as far back as 1552 (Brown, 1927). The alluvial deposits close to the coastline indicate regions where the sea, at spring tides and especially during storm surge conditions, was driven inland to inundate the marshes. Vast drowning of marshland and replenishment of lagoons with saline water is likely to have occurred with the concurrent distribution of the cockle from lagoon to lagoon.

J.T. Greensmith and E.V. Tucker (personal communication) have located a bed of C. glaucum shells now some two miles inland north of Burnham-on-Crouch, Essex. These shells are regarded as in a life assemblage and are found in the bank of a modern drainage ditch. The creation of sea defences no doubt effectively reduced the number of, and isolated, separate lagoon populations of C. glaucum. The living populations of C. glaucum in southern England are thus regarded as remnants of a much wider distribution.

This explanation of the distribution of C. glaucum cannot however be extended to include the occurrence of C. glaucum elsewhere in the British Isles. In Ireland a different origin and mode of dispersion is possible. Although southern and eastern Ireland are similar geologically in many ways to south east England, live C. glaucum populations were not discovered in this region, although apparently suitable localities were investigated. These pools contained other invertebrates commonly associated with C. glaucum in lagoons from other parts of the British Isles, but C. glaucum itself was absent. Yet nine localities have been discovered in the extreme west of Ireland, supporting an original observation of C. glaucum from the Isle of Great South Arran in Galway Bay, reported by Forbes & Hanley (1853). Thus, the distribution of C. glaucum in Ireland does not parallel the distribution in England. In fact, the reverse is true as only the west coast of Ireland appears to have been colonised.

The presence of C. glaucum on the western coast of the British Isles was not anticipated in this research and is regarded as particularly interesting. Bowden & Heppell (1968) record C. glaucum from North and South Uist in the Outer Hebrides. These specimens were collected from Loch an Duin, Trumisgarry in 1933 and from Loch Bee, South Uist in 1967 by A.R. Waterston, (Bowden & Heppell, 1968); but these specimens have not

---

• Bowden & Heppell regard the specimen figured by Tebble (1966) p. 105 (Fig. 55b) as a 'thin-shelled' C. edule. In fact the Cerastoderma collected from the River Roach are all 'thick-shelled' and the figure of Tebble is of a C. glaucum individual from the mixed population in that estuary.

been examined by tho author. It is strange that Nicol (1936) working on brackish water lochs of North Ulst, including Loch an Duin, from 1933-1935 does not record C. glaucum in the fauna, although she is particularly thorough in her ecological examination of these lochs. She states C. edule to be present in the middle basin of Loch an Duin along with fauna and flora which elsewhere occur in either estuarine or lagoon locations. However, C. edule is not recorded from the entrances of the loch which are more saline and tidal, and where C. edule would be expected to occur. The salinity of the middle basin was relatively constant between 26.2 amd 27.6‰ and it appears from Nicol's account that there is no tide in the middle basin. This evidence suggests that the cockles present were in fact C. glaucum and not C. edule.

It appears then, that some western lochs and lagoons stretching from the Hebrides south down western Ireland, through Connemara (where 3 sites occur) to Galway Bay (where 4 sites occur) and on to Chapeltown, Kerry and Rosscarbery, Cork, are colonised by C. glaucum. Thus the distribution of this cockle is wide but discontinuous on the western coasts.

Along these western shores the sea defence systems have not been constructed tothe extent they have in south-east England. Also, there is no reason to suppose that C. glaucum along these coasts has ever been more extensively distributed than it is at present. Therefore, explanation of the distribution of the cockle with reference to 'remnant populations' is not applicable. The fact that there is a possibility of interchange between lochs and lagoons which are renewed at spring tides supports the idea of dispersion by larvae. However, in the cases of totally land locked lagoons, e.g. Finavarra, the chances of C. glaucum larvae being introduced at the time of lagoon origin must be fairly remote.

Complete discussion of the distribution of C. glaucum requires a knowledge of the geographical origin of this cockle. In Europe there are two major stocks of C. glaucum - the Mediterranean and the Baltic Seas. It is likely that the species radiated from one or both of these two nuclei. Thus, the populations of C. glaucum on the western British coasts could have originated from either of these population centres.

A distinguishing characteristic of young C. glaucum, in contrast to C. edule, is the presence of spat and juveniles suspended in fine algae, normally Chaetomorpha. This has frequently been observed by the author and is even noted as far back as 1853 by Forbes and Hanley. Høpner-Petersen (1958) states that C. lamarcki (= C. glaucum) is often found 'hanging onto vegetation by its byssus threads', and this ability of C. glaucum to move by byssus was the original indication of the non-homogenetity of the Danish cockles being examined by Høpner-Petersen and Muus, (Muus, 1967). Thus, it is possible that C. glaucum in the western coast localities could be explained by 'passive' dispersal, fortuitously attached to sea birds legs. Certainly, the chances of Chaetomorpha, a fine thread like algae becoming entwined around the feet of sea birds is probably high, whilst the common occurrence of spat sized cockles in the alga lends weight to the hypothesis. Moreover many sea birds, geese and duck migrate from Northern Europe, south-westwards across the northern and western coasts of the British Isles. Nicol (1936) states that migrating geese cross northern Scotland and the Hebrides and this has been reiterated by Hunter and Warwick (1957). Thus, dispersal from the Baltic stock may be feasible even if seemingly unlikely. 'Passive' dispersal by birds is naturally extremely difficult to authenticate. Colonisation by fish, for example, of gravel pits, which are isolated from river systems, is probably attributable to transference of fish eggs by

birds. Dissemination of some terrestrial plants depends upon the attachment of seeds to the fur and feathers of animals or birds. Hunter, Maitland and Yeoh (1964) describing the occurrence of Potamopyrgus jenkinsi in the Loch Lomond area, give what they regard as an authentic example of 'passive' transport. They record the presence of a single living Littorina obtusata, a marine littoral gastropod, in a fresh water river, 13 miles from the nearest shore population of that species. This they attribute to dispersion by gulls and extend the argument to explain the occurrence of P. jenkinsi in the Loch Lomond region. Originally Nicol (1936) had accounted for the presence of P. jenkinsi in the Outer Hebrides by this theory. Thus the spread of C. glaucum could have occurred south-westwards from the Baltic to north-western and western coasts of the British Isles facilitated by 'passive' dispersal.

An alternative theory to account for the presence of C. glaucum on the western British Isles coasts is to consider origin from the Mediterranean C. glaucum. Unfortunately, there does not seem to be a method of separating morphologically the two stocks of C. glaucum from the Baltic and the Mediterranean seas. Possibly more sophisticated biochemical techniques will yield a method of separation in the future.

The so called 'Lusitanian' current initially flows westwards from the Straits of Gibraltar. This very saline but warm water forms a deep current, part of which then flows northwards at a depth of c.950 meters through the Bay of Biscay. (Sverdrup, Johnson & Fleming, 1942; Raymont, 1963). This water becomes progressively more shallow and occasionally surfaces off western Ireland. Hardy (1956) records that the northward extent of this current varies from year to year, on years of weak flow barely reaching 53°N. latitude (equivalent to half-way up Ireland), whilst on some years the 'Lusitanian' element of the plankton fauna can be

detected even in the Northern North Sea (Fraser, 1962). Upon surfacing the general trend of the North Atlantic Drift and coast currents could result in larvae being swept onto the western Irish and Hebridean coasts. Certainly Fraser (1962) notes the presence of indicator species of the Lusitanean current in tidal streams approaching the north-western Donegal coasts in May and June. Edwards (1968) relating water movements to the distribution of hydromedusae also recognises that a branch of the North Atlantic Drift forms a southerly-going current which forms an anti-clockwise swirl off western Ireland, running onto the Galway-Connemara coasts, (see Edwards - Generalised chart of the non-tidal circulation of the upper water layers. p. 333. Fig. 1). It is very interesting to note that Fraser (1955) records the presence of Ethmodiscus gazellae a large Mediterranean diatom as far north as 47°40' N., 13°58' W. off the Brittany coast, of France and he regards it as 'probably of direct Mediterranean origin'. Further, Wheeler (1970) reports the occurrence of three specimens of the goby Gobius cruentatus in south-western Irish waters. This goby occurs in the Mediterranean and is also found on the Spanish and Portugese Atlantic coasts. He discounts dispersal by planktonic larvae in water currents, noting that the surface currents from the north Spanish coasts do not run northwards, but that the general trend is eastwards up the English Channel. He does not, however, consider the possibility that the origin of this species in Irish waters could be from the Mediterranean population of the goby, via the deeper 'Lusitanian' current.

Any theory relying upon dispersion via currents requires the presence of a prolonged larval existence by the species. A journey in the region of 1,200 miles by slow water currents would probably be extending the

credulity of larval tolerance and capabilities to the extreme. Nevertheless, the fauna and flora of the south-western ~~Ireland~~ Irish coasts ~~do~~ contain species which are either rare or ~~are~~ absent on other British coasts, (Southward & Crisp, 1954), but occur in more southern climes. Thus, Paracentrotus lividus is virtually confined to Ireland in the British Isles, its occurrence in Devon and Cornwall being very rare, (Mortensen, 1943; Southward & Crisp, 1954). Fraeger (1950) reviews the lusitanian-mediterranean element of the Irish fauna and flora but unfortunately considers in majority only the land animals and plants.

Information concerning the length of larval life of C. edule can be found in the literature but there are no records for C. glaucum. Lebour (1938) suggests that the larval life of C. edule extends over five weeks before metamorphosis, reaching c.300μ in size. Orton (1933) notes that spawning begins in April but spat first appears towards the end of June, a period of perhaps six weeks. Baggerman (1953), from measurements upon larval growth, estimates that spat transport after metamorphosis must be in excess of one month before permanent settlement. It is interesting that Barker - Jørgensen (1946) working at Kristineberg found a large difference in the size of cockle spat from 275 - 345μ. C. edule spat do vary in size depending upon the food available (Kreger 1940). However, the cockles used by Barker - Jørgensen may not have been from a homogeneous genetic stock as both C. edule and C. glaucum occur at Gullmar's fjord, Sweden, for example, where some of his measurements were made, (Fohlo, 1963). This could suggest that the length of larval existence of the two cockles may not be identical.

Neither is there much information concerning the settlement of cockles. Gregariousness, recognised in so many invertebrate larvae may be an important factor in the settlement of lamellibranchs including the

Cerastoderma. Certainly the settlement of lamellibranch larvae is not as simple as is often maintained. The presence of byssus threads in young C. glaucum may be shown to be important in the settlement of this cockle, which may differ radically from C. edule which has not been recorded to exhibit a byssus.

It is interesting to note that various substances have been shown to shorten or lengthen larval pelagic life, (Wilson, 1952). An excess of calcium prolonges swimming and inhibits metamorphosis in some larvae, (Lynch, 1947), whilst for ascidians, Berrill (1930) demonstrated that hyperalkaline sea water tended to inhibit the metamorphosis of Phallusia, Ascidiella and Ciona larvae. It is likely then that factors hithertoo unrecognised could affect the length of larval life.

Many invertebrate larvae postpone metamorphosis into adults until a suitable substrate for settlement has been discovered, (Mortensen, 1921; Thorson, 1946). Wilson (1932) showed that Mitraria larvae of the polychaete Owenia fusiformis metamorphosed only when stimulated to do so by fine sand. However, the period of delay was only recorded as a few days. A similar situation had previously been demonstrated in echinoderm larvae by Mortensen (1921). Day & Wilson (1934) also found that the retention of larval life could be extended for several weeks in Scolecolepis fuliginosa. Thus, in general, Wilson (1952) showed that the end of planktonic life of a benthic species is a searching phase and metamorphosis can be postponed until tidal currents happen to carry the larvae to a favourable place. Balanus balanoides is able to postpone metamorphosis for several weeks, (Knight-Jones & Moyse, 1961), whilst Wilson (1970) has recently shown that larvae of Sabellaria alveolate can delay metamorphosis for four weeks and still develop normally, while the larvae of both S. alveolate and S. spinulosa have been maintained in

the laboratory for over nine and seven months respectively before metamorphosis. It is suggested by Wilson (1952) that the giant larvae of littoral crustacea taken in deep water well away from land, recorded by Gurney (1942), are individuals which have failed to metamorphose into adults ~~because of failure of metamorphosis.~~

In the absence of information concerning the larval life of C. glaucum it can only be suggested that this cockle may be different from C. edule in many aspects of settlement and thus may be able to postpone metamorphosis. Perhaps the occurrence of this cockle predominantly in lagoons may indicate that stagnant water conditions are a necessary requirement for initiation of metamorphosis from a larval stage.

However, apposing the general idea of transportation by ocean currents is the fact that normally C. glaucum does not occur where there is wave-action or extensive tidal movements. It may be discovered that C. glaucum larvae cannot survive in the open sea where large scale water movements occur. A long period of planktotrophic life increases the danger from predation and the possibility of starvation, if the correct food organisms are not in abundance. Finally, no records have been discovered by the author of larvae of mediterranean littoral or sub-littoral organisms in the Lusitanian current. This may reflect, however, not the absence of these larvae, but more the lack of investigation into the smaller constituents of this current which may occasionally be present.

If this latter theory is correct, then C. glaucum may well be yet another example of a member of the western Irish fauna which has originated from more southern climes.

REFERENCES

(for Sections II, III and IV not cited in references to Section I.)

BAGGERMAN, B., 1953. Spatfall and transport of Cardium edule L. Arch. Neerl. Zool. Vol. 10, pp. 315-342.

BARKER-JØRGENSEN, C., 1946. Lamellibranchiata. In 'Reproduction and larval development of Danish marine bottom invertebrates'. (by G. Thorson) pp. 277-311. Medd. Fra. Komm. Dan. Fisk-og. Havunders, serie: Plankton, Bind 4, N.R.1.

BATESON, W., 1889. On some variations of Cardium edule apparently correlated to the conditions of life. Phil. Trans. Roy. Soc., Lond., series B, Vol. 180, pp. 279-330.

BERRILL, N.J., 1930. Studies on tunicate development. I. General physiology of development of simple ascidians. Phil. Trans. Roy. Soc. London, ser. B. Vol. 218, pp. 37-79.

BROWN, E., 1927. An Essex Island Parish. Essex Review, Vol. 36, p. 176.

COBB, R.T., 1956. Shingle Street, Suffolk: a brief geographical introduction. Report Field Studies Council for 1956-57, pp. 31-42.

COLE, H.A., 1956. A preliminary study of growth rate in cockles (Cardium edule L.) in relation to commercial exploitation. J. Cons. perm. int. Explor. Mer. Vol. 22, pp. 77-90.

COLE, H.A., 1969 (written communication).

COLES, R., 1936. The evolution of the coastal drainage of Essex. Essex Nat. Vol. XXV, part II 1935-36, pp. 36-49 and 65-70.

CREEK, G.A., 1960. The development of the lamellibranch Cardium edule L. Proc. Zoo. Soc. Lond. Vol. 135, pp. 243-260.

DAHL, E., 1956. Ecological salinity boundaries in Poikilohaline waters. Oikos, Vol. 7(1), pp. 1-21.

DAY, J.H. & NELSON, D.R., 1934. On the relation of the substratum to the metamorphosis of Scolecolepis fuliginosa (Claparède). J. mar. biol. Ass. U.K., Vol. 19, pp. 655-662.

EDWARDS, C., 1968. Water movements and the distribution of Hydromedusae in British and adjacent waters. Sarsia. Vol. 34, pp. 331-346.

EKMAN, S., 1953. The Mediterranean. Atlantic fauna and the Sarmatic fauna. Zoogeography of the Sea, (translation by Palmer, E.) Sidgwick and Jackson, London (1953), pp. 80-99.

ELLIS, A.E., 1932. The habitats of Hydrobiidae in the Adur estuary. Proc. Malacol. Soc. Lond., Vol. 20, pp. 11-18.

FEATHERSTONE, A., 1968. 'Abraham's Bosom'. The Conch. Soc. of Gt. Britain and N.I., Newsletter No. 27, pp. 66-68.

FRASER, J.H., 1955. The Plankton of the waters approaching the British Isles in 1953. Scottish Home Dept. Marine Res. No. 1, pp. 1-12. Her Majesty's Stationery Office.

FRASER, J.H., 1962. 'Nature Adrift'. Foulis & Co., London.

GREENSMITH, J.T. & TUCKER, E.V., 1970. (Proc. Geol. Assoc. - in prep.)

GRIEVE, H., 1959. The great tide. Essex County Council.

GURNEY, R., 1942. Larvae of decapod crustacea, Ray. Society, London.

HAMMOND, A., 1969. (written communication).

HARDY, A., 1956. 'The Open Sea': Its Natural History, Part 1: The world of Plankton. Collins, London.

HØPNER-PETERSEN, G., 1968. (written communication).

HOWES, N.H., 1939. The ecology of a saline lagoon in South-east Essex. J. Linn. Soc. Zool., Vol. 40, pp. 383-445.

HUNTER, W.R., MAITLAND, P.S. & YEOH, P.K.H., 1964. Potamopyrgus jenkinsi in the Loch Lomond area, and an authentic case of passive dispersal.

HUNTER, W.R. & WARWICK, T., 1957. Records of Potamopyrgus jenkinsi (Smith) in Scottish fresh waters over fifty years (1900-1956). Proc. Roy. Soc. Edinb. (B) Vol. 66, pp. 360-373.

JEFFREYS. 1863. British Conchology. The Mollusca, Vol. II - Marine Shells, London.

JOHNSTON, J., L.M.B.C. Memoirs Vol. II, Cardium. Lobb, Liverpool (1899)

KNIGHT-JONES, E.W. & MOYSE, J., 1961. Intraspecific competition in sedentary marine animals. Symp. Soc. Exp. Biol. Number XV, Mechanisms of biological competition, pp. 72-95.

KRUGER, J., 1940. On the ecology of Cardium edule L. Arch. Néer. Zool. Vol. 4, pp. 157-200.

LEBOUR, M.V., 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae. J. mar. biol. Ass. U.K. Vol. 23, pp. 119-145.

LYNCH, W.F., 1947. The behaviour and metamorphosis of the larva of Bugula neritina (Linnaeus): Experimental modification of the length of the free-swimming period and the responses of the larvae to light and gravity. Biol. Bull. mar. Lab., Woods Hole, Vol. 92, pp. 115-150.

MORTENSEN, T., 1921. Studies of the development and larval forms of Echinoderms. G.E.C. Gad., København.

NICHOL, E.A.T., 1936. The brackish-water lochs of Orkney. Proc. Roy. Soy. Edinb., Vol. 56 (1935-1936), pp. 169-195.

OCKELMANN, W.K., 1958. Marine lamellibranchiata. Meddr. Gronland, Vol. 122, no. 4, p. 198.

ORTON, J.H., 1933. Summer Mortality of cockles on some Lancashire and Cheshire Dee Beds in 1933. Nature Vol. 132, pp. 314-315.

PHOLO, R.H., 1963. Notes on the discrimination between Cardium edule and Cardium lamarcki. Cah. Biol. Mar., Vol. 4(2), pp. 177-182.

PRAEGER, R.C., 1950. Natural History of Ireland. London: Collins.

PURCHON, R.D., 1939. The effect of the environment upon the shell of Cardium edule. Proc. Malacal. Soc. Lond. Vol. 23, pp. 256-267.

RAYMONT, J.E.G., 1963. Plankton and Productivity in the oceans. International series of monographs on pure and applied biology. General Ed., G. Kerkut. Pergamon Press, 1963.

REMANE, A., 1934. Die Brackwasserfauna (mit besonderer Berucksichtigung des Ostseegebietes). Verh. Deutsch Zool. Ges. 36.

REMANE, A., 1940. Einfuhrung in die Zoologische Okologieder Nord und Ostsee. Tierw. Nord.-U. Ostsee. Lief. 34.

SORBY, H.C., 1906. On the salinity of the seawater along the coast of Essex. Essex Nat. Vol. XIV(7), pp. 235-236.

SOUTHWARD, A.J. & CRISP, D.J., 1954. The distribution of certain intertidal animals around the Irish Coast. Proc. R. Ir. Acad. Vol. 57, (1)(B), pp. 1-29.

SVERDRUP, H.U., JOHNSTON, M.W. & FLEMING, R.H., 1942. The Oceans, Englewood Cliffs, Prentice Hall, p. 646 and pp. 685-686.

THORPE, W.H., 1927. The fauna of brackish pools on the Sussex coast. South-east Naturalist, Vol. 23, pp. 27-29.

THORSON, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates. Medd. Fra. Komm. Dan. Fisk-og. Havunders serie: Plankton, Vol. 4, N.R.1.

VALIKANGAS, I., 1933. Ueber die Biologie Ostsee als Brackwassergebiet. Verh. Int. Ver. Theor. u. Angew. Limnologie, Vol. 6.

WHEELER, A., 1970. Gobius cruentatus - a fish new to the northern European fauna. J. Fish. Biol. Vol. 2, pp. 59-67.

WILSON, D.P., 1932. On the Mitraria larva of Owenia fusiformis Della Chiaje. Phil. Trans. Roy. Soc. Lond. ser. B. Vol. 221, pp. 231-334.

WILSON, D.P., 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of Ophelia bicornis Savigny. Ann. Inst. Oceanog. Vol. XXVII, pp. 49-156.

WILSON, D.P., 1970. The larvae of Sabellaria spinulosa and their settlement behaviour. J. mar. biol. Ass. U.K., Vol. 50(1), pp. 33-52.

SECTION - V

SECTION V

COMPARATIVE STUDIES OF THE MIXED CLEYSTOCENE POPULATIONS OF THE CROUCH AND ROACH ESTUARIES, ESSEX, TOGETHER WITH SOME REFERENCE TO VARIOUS SINGLE COCKLE POPULATIONS.

1. Demographic properties of the Crouch mixed population.

During the investigation of the reproductive cycles and symbiont faunas of the mixed cockle population of the Crouch estuary, additional investigations were undertaken concerning the ages and sizes of the two cockles.

a) Annual rings, disturbance rings and age structure of the Crouch cockle populations.

The use of annual shell rings as a means of establishing age has been employed in a variety of molluscs: Cardium edule (L.), Orton (1926); Venerupis pullastra (Montagu), Quayle (1951 - 2); Placopecten magellanicus, Stevenson & Dickie (1954); Scrobicularia plana (da Costa), Green (1957); Pecten maximus (L.), Mason (1957); Macoma balthica (L.), Segerstråle (1960); Mytilus edulis (L.), Seed (1969) and Tellina tenuis (da Costa), McIntyre (1970). During the winter months, and perhaps in periods of exceptional circumstances, the mantle edge is withdrawn from the shell margins, causing a cessation of shell growth. However, the innermost nacreous layer is continually deposited (Seed, 1969). Thus, when growth is resumed, old and new regions of the shell are not continuous, resulting in a disturbance ring.

It was first shown by Orton (1926) that the shell of C. edule exhibits a well marked series of rings, which represent annual periods of growth cessation, associated with the colder months of the year.

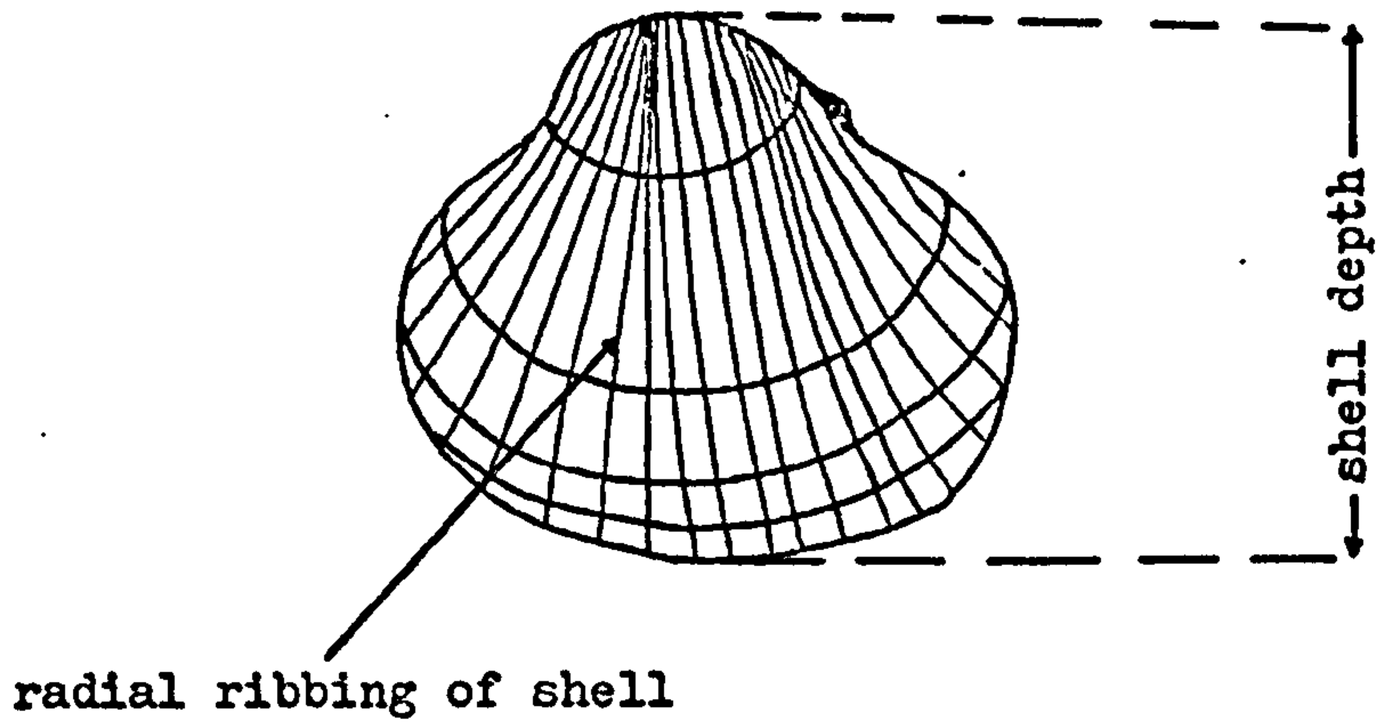
He qualified this, however, by noting the presence of disturbance rings which could be produced by various environmental irregularities e.g. gales, shifting substratum, and even removing the cockles from their habitat for a short period. Nevertheless these disturbance rings are generally less prominant than the true annual rings, and usually do not completely encircle the shell, tending to fade away at the margins (Cole 1956). Thus upon the simple picture of annual winter-ring, may be super-imposed additional rings, not related to the growth rate of the cockles.

In older cockles, the umbo region of the shell is often worn, and thus the first ring laid down during the first winter may be obliterated. This feature has also been observed in the Canadian littoral cockle Cardium corbis (Fraser 193X[2]). However, the growth rate in the second year is always large, thus the shell laid down during the second summer is proportionately greater. In the first summer, the growth rate is also correspondingly large, but the period of growth is less, as spatfall does not occur until after mid-June. By the third growing season the rate of shell deposition has slowed, and this is reduced proportionately as the cockle ages - see diag.1 and plate 1. By determining the position of the greatest growth increment, the location of the first winter ring can be accurately determined, or deduced if shell abrasion has been excessive. (For initial assistance of ageing cockles I am indebted to Mr.G.Pickett of Burnham Shellfish Laboratory, Burnham-on-Crouch, Essex).

In the Crouch, mixed cockle population both C.edule and C.glaucum exhibit strong annual rings in all year classes, however distrubance rings are sometimes present. Cockles of both types were collected from a limited area at extreme Low Water Spring Mark in May 1968. Some 550 C. edule and 672 C. glaucum were collected and aged. The age

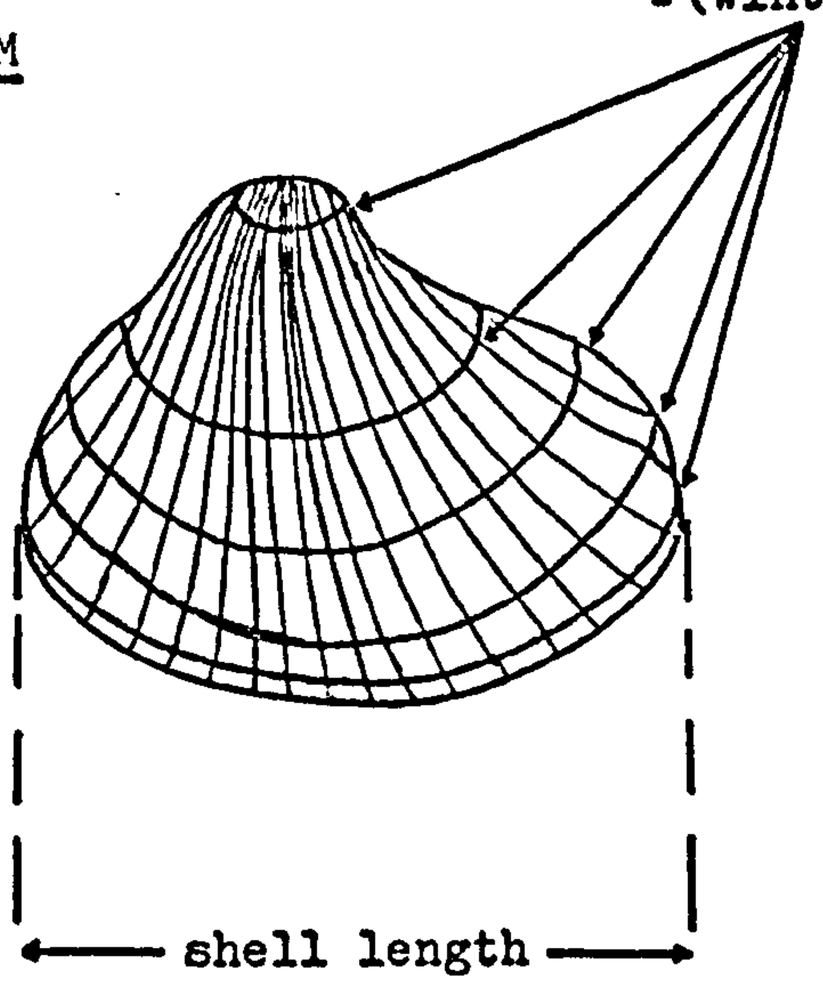
Diagram 1

C.EDULE



annual rings
=(winter growth checks)

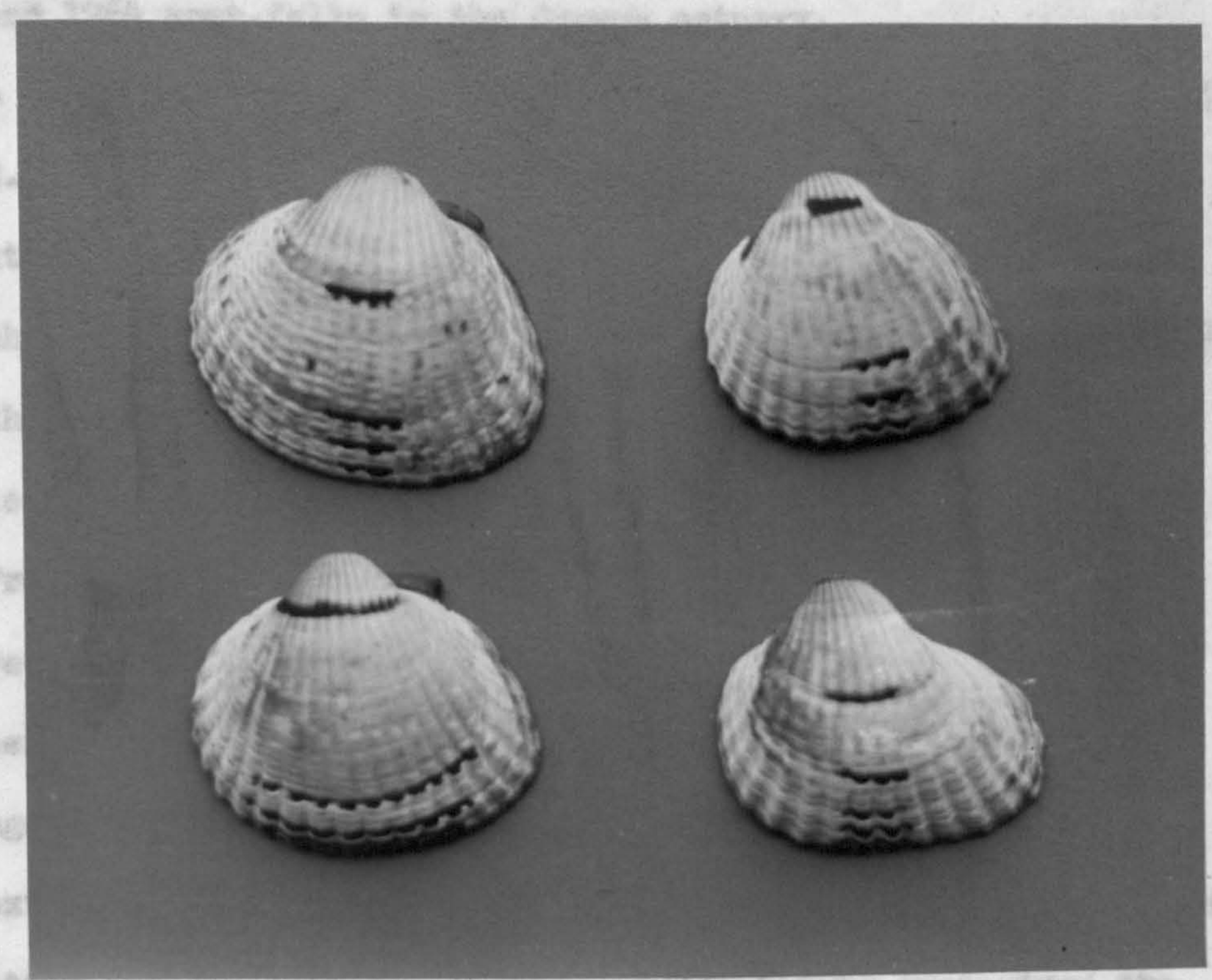
C.GLAUCUM



Schematic diagram of cockles displaying external shell characteristics, and the shell parameters of length and depth.

Plate 1

Plate 1 - Annual rings found on the shells of the *Cerastoderma* collected from the Crouch mixed cockle population.



C. EDULE *C. GLAUCUM*

distributions are shown in figure 1. A similar pattern is found in both cockles; with a marked reduction in the numbers of 5 and 6 year old individuals. The reduction in numbers of the subsequent year classes after the 5-ring cockles, is thought to correspond with the high nortality of the cockles during the exceptionally cold winter of 1962/3, and the large number of 4 and 5 year old individuals indicates the success of the 1963 and 1964 spat-falls in the Crouch estuary.

The effect of very cold winters upon the littoral fauna is well documented. Crisp et al. (1965)[4] reviews the effects of the 1962/3 winter and records extensive mortalities in various C. edule populations around the English coasts e.g. Whitstable, Kent. Franklin and Pickett (1968) studying the cockle resources of the Wash area, noted that there has been little recruitment of the stocks since the outstanding spat-fall of 1963, from which most of the cockle beds in England and Wales have been derived. Thamdrup (1935) concluded that the severe winter of 1928/9 exterminated a great part of the C. edule in the German Wadden Sea at Skallingen, but noted that this had been followed in the next two years by extensive settlement and that these cockles had then dominated the population for the next few years. Smidt (1944) summarised the effects of this cold winter, and suggested that there was an inverse relationship between the numbers of established cockles and numbers of settling individuals. Thus it appears that fluctuations in cockle population density are cyclical, and have been shown to be reproduced on widely separated beds. The similarity between the age structure of the Crouch estuary and the German Wadden Sea, in relation to the affects of a severe winter, suggests that the Crouch cockles have been correctly aged.

Annual rings were recognised in all other populations of C. edule from south-east England. Stephen (1931 , 1932) was unable to discern the 1st annual ring of cockles collected from the Clyde estuary, whilst

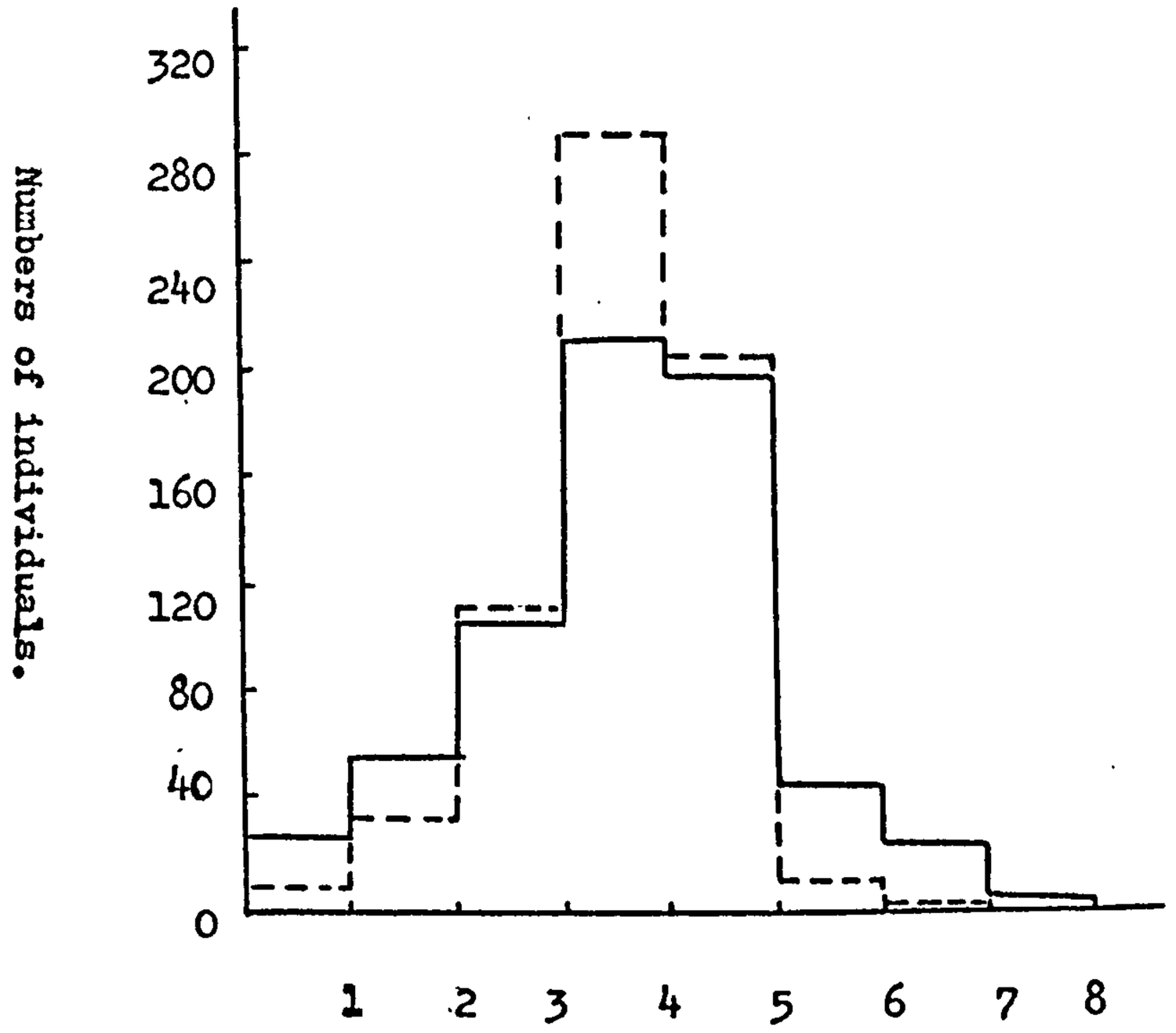


Fig. 1 - Age structure of the populations of C.edule and C.glaucum from the Crouch estuary.

——— = C.edule

– – – – = C.glaucum

Kreger (1940) working on the Dutch Wadden Sea, noted the difficulty in ageing cockles from high tidal levels, where long periods of aerial exposure occur. The C. edule collected from above M.T.L. from Chapeltown, Eire, also exhibit confused annual rings, and this is associated with stunted overall growth.

Cole (1956) records that the growth-rings of young cockles from Poole Harbour, Dorset are faint or absent and he suggests that this is related to the short duration of the cold winter period, and the relatively high winter temperatures of this locality. However, annual rings are clearly visible upon the shell of older individuals. It may be a combination of the peculular tidal conditions in Poole Harbour, and less cold winters with rapid shell growth which ~~result in~~ Causes the faint first and second rings in Poole cockles.

Lagoon populations of C. glaucum do not show regular winter rings and therefore cannot be reliably aged. Growth checks that ~~what~~ do exist are often extremely ill-defined and very faint. The relative shortness of the winter in marine pools, which quickly warm up in the spring may explain the lack of rings, but on the other hand permanent submersion may effect the daily rhythm of shell deposition. This rhythm has been shown by House & Farrow (1968) in littoral C. edule and it may be that for pronounced annual rings, periodic exposure to air is required. As an environment, lagoons are far more stable than the shore, altering only slowly over a relatively long period of time. The formation of annual rings requires the removal of the mantle edge from the shell periphery, and it may be that on the shore, stimuli causing this reaction are more likely to occur in the form of stresses and rapid changes, that in pools.

Orton et al (1937) however record the presence of annual rings in C. edule collected from the bottom of a marine 'lake' constructed near high-water mark on the Lancashire coast. These cockles were usually ~~permanently~~ submerged, but once every year, about February, the lake was

drained for inspection. This period of disturbance, and exposure to cold aerial conditions, may have been sufficient to stimulate the formation of a pronounced annual ring in these cockles.

Thus littoral C. edule normally exhibit prominant annual winter-rings whereas lagoon C. glaucum generally do not. Both cockle types from the Crouch mixed population exhibit annual rings. There does not appear to be a radical difference in the population age structure between C.edule and C. glaucum which suggests that spawning success and settlement are equally successful in the two cockles.

2. Comparison of sizes of C. edule and C. glaucum from the Crouch mixed population.

Cockles were collected during May and June 1968 from a small section of foreshore at Hullbridge 'ferry', River Crouch, at a single tidal level - E.L.W.S. Each cockle was measured from the umbo to shell periphery, along the 'middle rib,' (rib perpendicular to the longitudinal axis of the shell) see diagram 1). Thus the age of each cockle was almost exactly, that indicated by the number of winter rings on the shell. The shell depth (= height of some workers) was selected as the shell parameter for comparison between the two cockles, because shell width and length, have different relationships to tissue content in the two cockles. Shell depth, as will be shown later, is a reliable indicator of shell size in both Cerastoderma, as the relationship between tissue (flesh) weight and shell depth is similar in the two cockle types.

The relationship of shell depth to age is shown in fig. 2. In general, it can be seen that considering cockles of the same age C. glaucum is smaller than C. edule. It seemed possible that either the growth rate of C. glaucum was less than C. edule, or settlement of the spat occurred consistently later in C. glaucum, which would reflect in a smaller size throughout the following years.

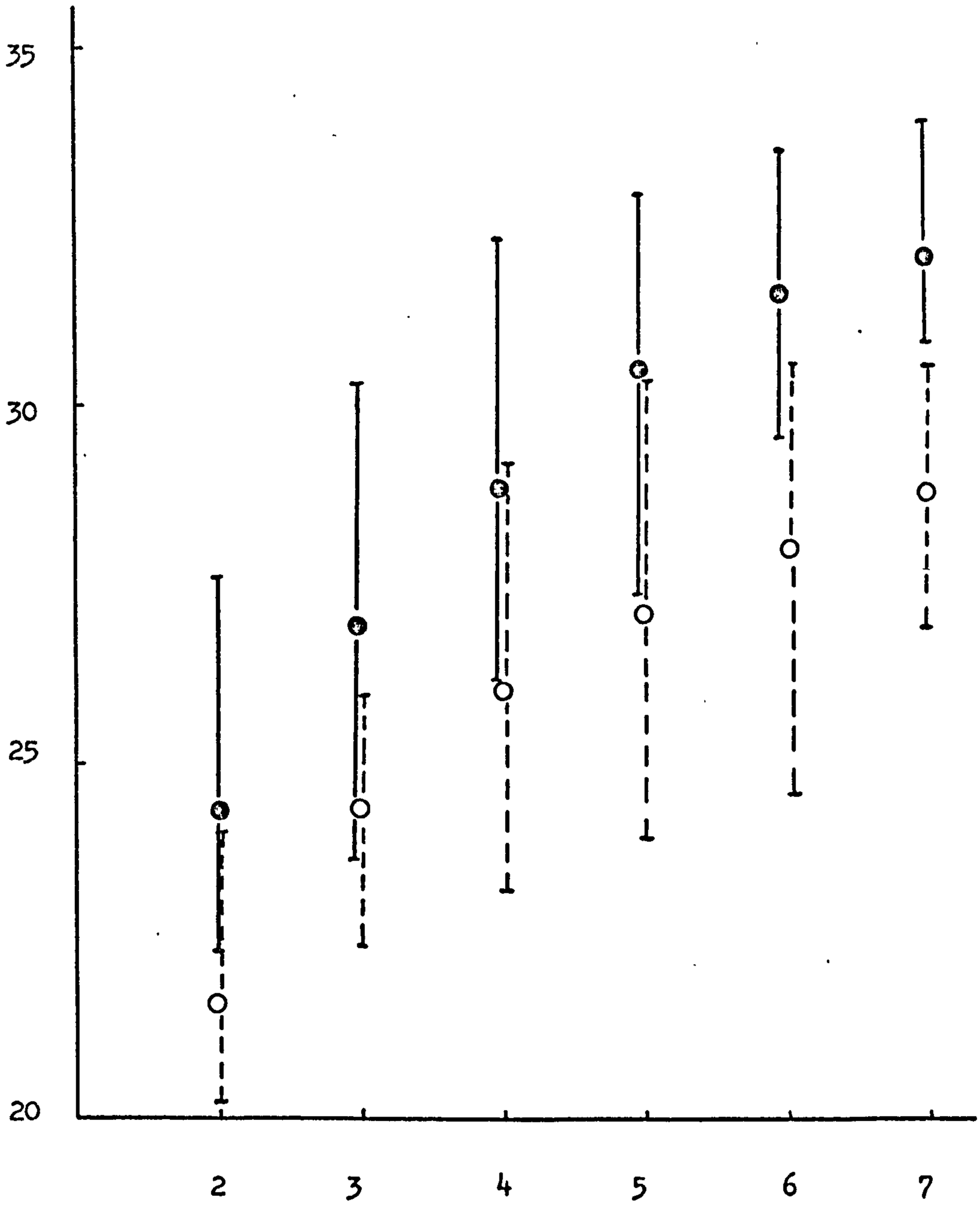


Fig 2 - Relationship of shell depth (mm's) to age in C.edule and C.glaucum from the Crouch mixed population.

● -- Mean shell depth and range of sizes of C.edule

○ -- Mean shell depth and range of sizes of C.glaucum

To answer this question all the annual rings present on the shells of two samples of cockles, collected on the 19. 6.68. and 26. 6.68. were measured to the nearest 0.05 mm. using vernier calipers. Both shell length and shell depth were determined for each annual ring. Thus the following information was available;-

(i) Relationship of shell length to age for the Crouch C. edule which could then be compared with information available in the literature.

(ii) Comparison of average shell sizes, length and breadth with age, for the two cockles.

(iii) Average growth increments of the two cockles over successive years.

The data from these measurements is shown in tables 1 and 2.

(i) Length to age relationship of Crouch C. edule compared with values available for C. edule in the literature.

The range of sizes for each age of cockle recorded in the literature is displayed in table 3. It can be seen that the Crouch C. edule fall approximately mid-way in the size ranges recorded, and this is further evidence indicating that the Crouch cockles were being correctly aged.

(ii) Comrison of shell size with age for the two cockle types.

The average relationship of shell length and shell depth to age is shown in figures 3 and 4. The cumulative increase represents a curve of absolute growth. The consistently larger size of C. edule is again well displayed by this averaged data. It can be seen, particularly in the case of shell depth, that the difference between C. edule and C. glaucum remains fairly constant in cockles of different ages and does not increase progressively. The difference in shell depth between the two cockles from the first to sixth years are: 6.0, 6.5, 4.8, 4.0, 4.1, 4.7 mm's respectively.

Table 1 Average shell lengths in mm's and growth increments of the two Cerastoderma collected from the Crouch mixed cockle population.

A) Cerastoderma edule

Growing year of first summers growth.	Numbers examined	Size of 1st ring	Growth -mm's	Size of 2nd ring	Growth -mm's	Size of 3rd ring	Growth -mm's	Size of 4th ring	Growth -mm's	Size of 5th ring	Growth -mm's	Size of 6th ring	Growth -mm's	Size of 7th ring
1967	10	18.2	-	-	-	-	-	-	-	-	-	-	-	-
1966	10	18.8	8.2	27.0	-	-	-	-	-	-	-	-	-	-
1965	15	19.5	8.6	28.1	3.4	31.5	-	-	-	-	-	-	-	-
1964	19	17.4	10.7	28.1	3.8	31.9	1.3	33.2	-	-	-	-	-	-
1963	18	14.7	14.1	28.8	4.3	33.1	1.8	34.9	1.1	36.1	-	-	-	-
1962	10	16.5	10.7	27.2	4.5	31.7	2.7	34.4	1.2	35.6	1.2	36.8	-	-
1961	10	12.7	13.0	25.7	4.4	30.1	3.2	33.3	2.3	35.6	1.0	36.6	0.8	37.4
Mean values:-		16.8	10.9	27.5	4.1	31.7	2.2	33.9	1.5	35.8	1.1	36.7	0.8	37.4

B) Cerastoderma glaucum

Growing year of first summers growth.	Numbers examined	Size of 1st ring	Growth -mm's	Size of 2nd ring	Growth -mm's	Size of 3rd ring	Growth -mm's	Size of 4th ring	Growth -mm's	Size of 5th ring	Growth -mm's	Size of 6th ring	Growth -mm's	Size of 7th ring
1967	10	11.2	-	-	-	-	-	-	-	-	-	-	-	-
1966	10	12.7	8.1	20.8	-	-	-	-	-	-	-	-	-	-
1965	21	12.4	8.0	21.4	4.3	25.6	-	-	-	-	-	-	-	-
1964	20	11.9	9.5	21.5	4.7	26.2	2.1	28.3	-	-	-	-	-	-
1963	15	8.9	11.5	20.4	4.1	24.5	2.1	26.6	1.6	28.2	-	-	-	-
1962	10	9.0	8.7	17.7	6.6	24.6	3.4	28.0	1.5	29.8	1.2	31.0	-	-
Mean values:-		11.0	9.6	20.3	4.9	25.2	2.5	27.6	1.5	29.0	1.2	31.0	-	-

Table 2 Average shell depths and growth increments of the two Cerastoderma collected from the Crouch mixed cockle population, in mm's

A) Cerastoderma edule

Growing year of first summers growth.	Numbers examined	Size of 1st ring	Growth -mm's	Size of 2nd ring	Growth -mm's	Size of 3rd ring	Growth -mm's	Size of 4th ring	Growth -mm's	Size of 5th ring	Growth -mm's	Size of 6th ring	Growth -mm's	Size of 7th ring
1967	10	16.7	-	-	-	-	-	-	-	-	-	-	-	-
1966	10	17.3	8.3	25.6	-	-	-	-	-	-	-	-	-	-
1965	15	16.1	8.5	24.6	2.3	26.9	-	-	-	-	-	-	-	-
1964	19	16.5	9.4	25.9	2.7	28.6	1.3	29.9	-	-	-	-	-	-
1963	15	13.8	12.3	26.1	3.4	29.5	1.6	31.1	0.9	32.0	-	-	-	-
1962	10	15.6	9.2	24.8	4.0	28.8	1.6	30.4	1.2	31.6	0.9	32.5	-	-
1961	10	11.9	11.8	23.8	3.4	27.2	2.6	29.8	1.7	31.5	1.2	32.7	0.7	33.4
Mean values:-		15.4	9.9	25.1	3.2	28.2	1.8	30.1	1.3	31.7	1.1	32.6	0.7	33.4

B) Cerastoderma glaucum

Growing year of first summers growth.	Numbers examined	Size of 1st ring	Growth -mm's	Size of 2nd ring	Growth -mm's	Size of 3rd ring	Growth -mm's	Size of 4th ring	Growth -mm's	Size of 5th ring	Growth -mm's	Size of 6th ring	Growth -mm's	Size of 7th ring
1967	10	9.4	-	-	-	-	-	-	-	-	-	-	-	-
1966	23	10.7	8.9	19.6	-	-	-	-	-	-	-	-	-	-
1965	46	10.3	8.8	19.1	3.5	22.6	-	-	-	-	-	-	-	-
1964	20	11.1	8.1	19.9	4.2	24.1	1.7	25.8	-	-	-	-	-	-
1963	14	8.4	12.1	20.5	3.8	24.3	2.3	26.6	1.4	28.0	-	-	-	-
1962	10	6.7	7.3	14.0	8.6	22.6	3.2	25.8	1.4	27.2	0.7	27.9	-	-
Mean values:-		9.4	9.0	18.6	5.0	23.4	2.4	26.1	1.4	27.6	0.7	27.9	-	-

Table 3

Variation in length of C. edule of different ages from various localities,

in - mm's.

Location of population.	0-1 year group. 1- ring	1-2 year group. 2- rings	2-3 year group. 3- rings	3-4 year group. 4- rings	4-5 year group. 5- rings	Authority
River Yealm, Plymouth.	19 - 22 (max.27/28)	28 - 31 (max. 35)	36 - 37 (max. 43)	35 - 39 (max. 41)	41 - 45 (max.45/46)	Orton(1926)
Swansea Bay.	17.4	24.0	-	-	-	Wright(1926)
Maplin Sands.	11.1	-	22.0	28.0	-	
Lancashire coast.	13 - 15 mode 18.5	21 - 34. mode 27.5	21 - 38 mode 31.5	29 - 40 mode 35.1	- -	Orton et al (1937)
Dutch Wadden Sea.	19 - 22 (max.24/28)	28 - 32 (max.35/37)	33 - 36 (max. 38/43)	35 - 39 (max.41/45)	- -	Kreger(1940)
" "						
- littoral flat -	19.5	28.1	32.0	-	-	Kristensen (1956)
- living in creek -	14.0	20.6	25.6	-	-	
Range from a selection of sites around British coasts.	9.3 - 15.9	17.9-28.5	23.1-32.7	31.1-39.9	31.6-41.7	Cole(1956)
Llanrhidan sands.	12.6-13.4	21.1-24.0	26.0-26.9	28.2-29.2	29.7-29.8	Handcock (1965)
Summary of size ranges in literature:	9.3-22	19.9-31	21-38	28.2-40	29.7-45	
Average sizes of Crouch C.edule	16.8	27.5	31.7	33.9	35.8	

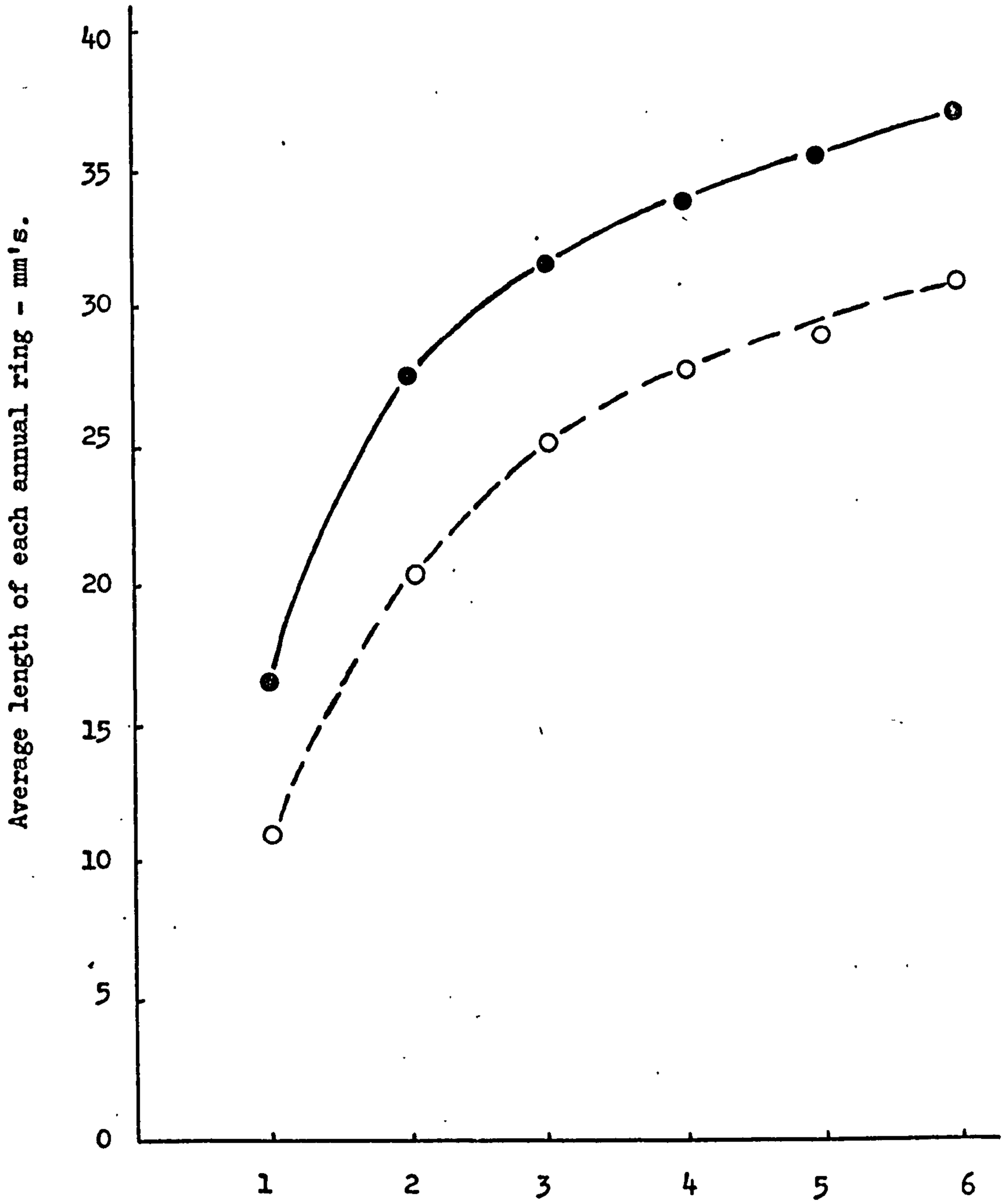


Fig 3 - Average length of each winter growth check on the shells of the two Cerastoderma collected from the Crouch estuary.

●——● - C.edule.

○— —○ - C.glaucum.

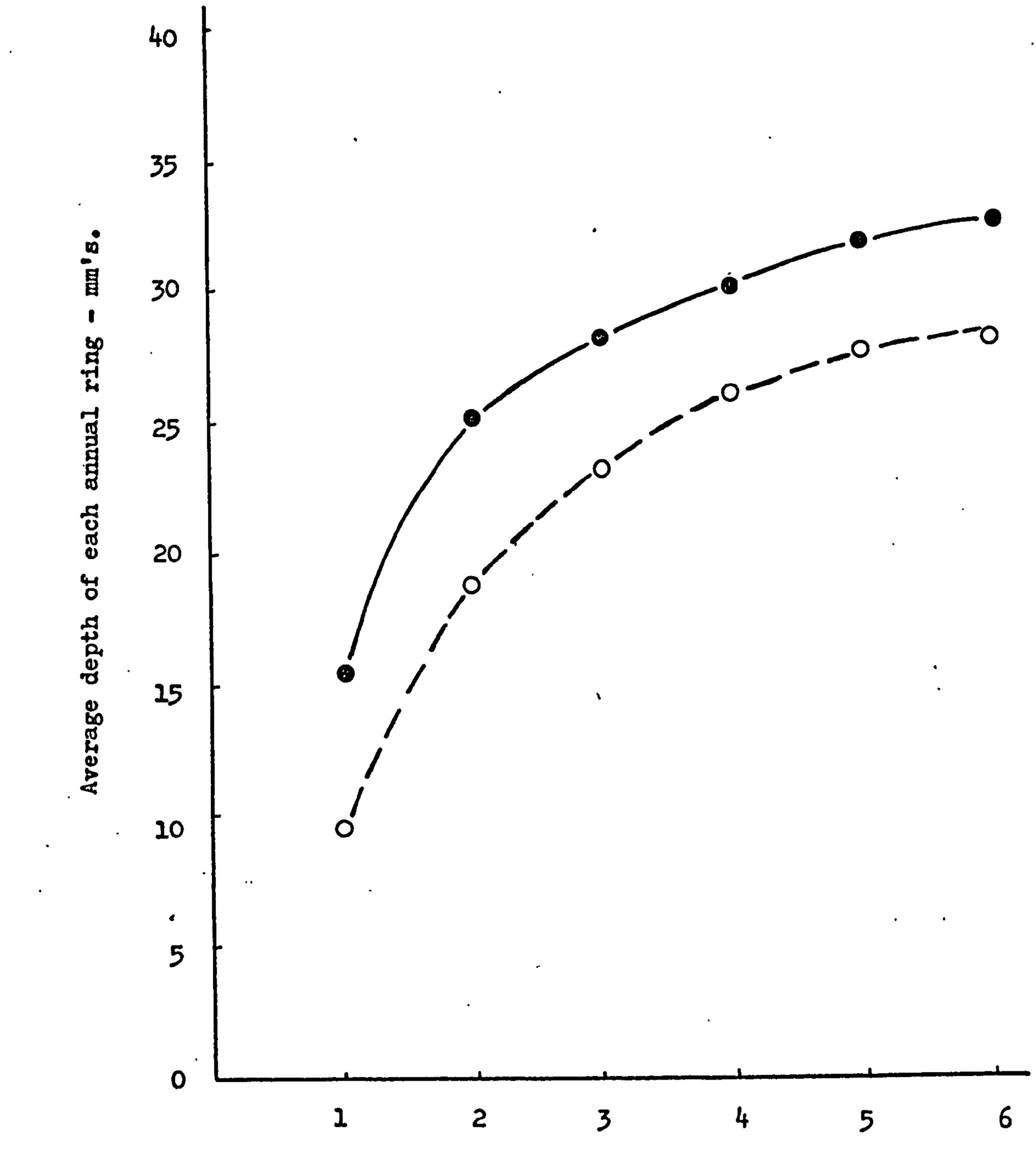


Fig 4 - Average depth of each winter growth check on the shells of the two Cerastoderma collected from the Crouch estuary.

●——● - C.edule.

○— —○ - C.glaucum.

These figures would not be expected to be identical as they are average results over several years, but they are close enough to indicate the absence of a progressive increase. It would seem therefore that there is an initial difference in the size of first year cockles, and that this is maintained over the subsequent years. This has been correlated with the fact that C. edule spawns on average seven weeks before C. glaucum (- see Reproductive cycles of the two Cerastoderma, Section VI), and thus settlement occurs earlier in C. edule. If the growing season extends to the end of October, C. edule has an 18 week growing period in the first year after settlement, whereas C. glaucum has only in the region of 11 weeks. Thus the length of the growing season of C. glaucum is 61.1% that of C. edule. The average first year shell depth of the two cockles is 15.4 and 9.4mm. for C. edule and C. glaucum respectively. The size of C. glaucum in the first year is on average only 61.0% that of C. edule. Thus there is clearly a good positive correlation of cockle size to estimated length of growing season after settlement in the two cockles.

(iii) Average growth increments of the two cockles over successive years.

The average growth increase between each annual ring, the relative growth rate, is graphed in figures 5 and 6. It can be seen that the growth rates of the two cockles are very similar suggesting that the observed differences in shell size are not due to differential growth throughout life.

It is evident that the second year growth, between the first and second annual ring, is slightly greater in C. edule than in C. glaucum, but that in subsequent years C. glaucum tends to have a slightly faster growing rate. However, C. edule is already appreciably larger than C. glaucum by the end of the first year, - see figures 3 and 4. It has been shown in C. edule from Llanrhidian sands by Hancock (1967), " - that the cockle population

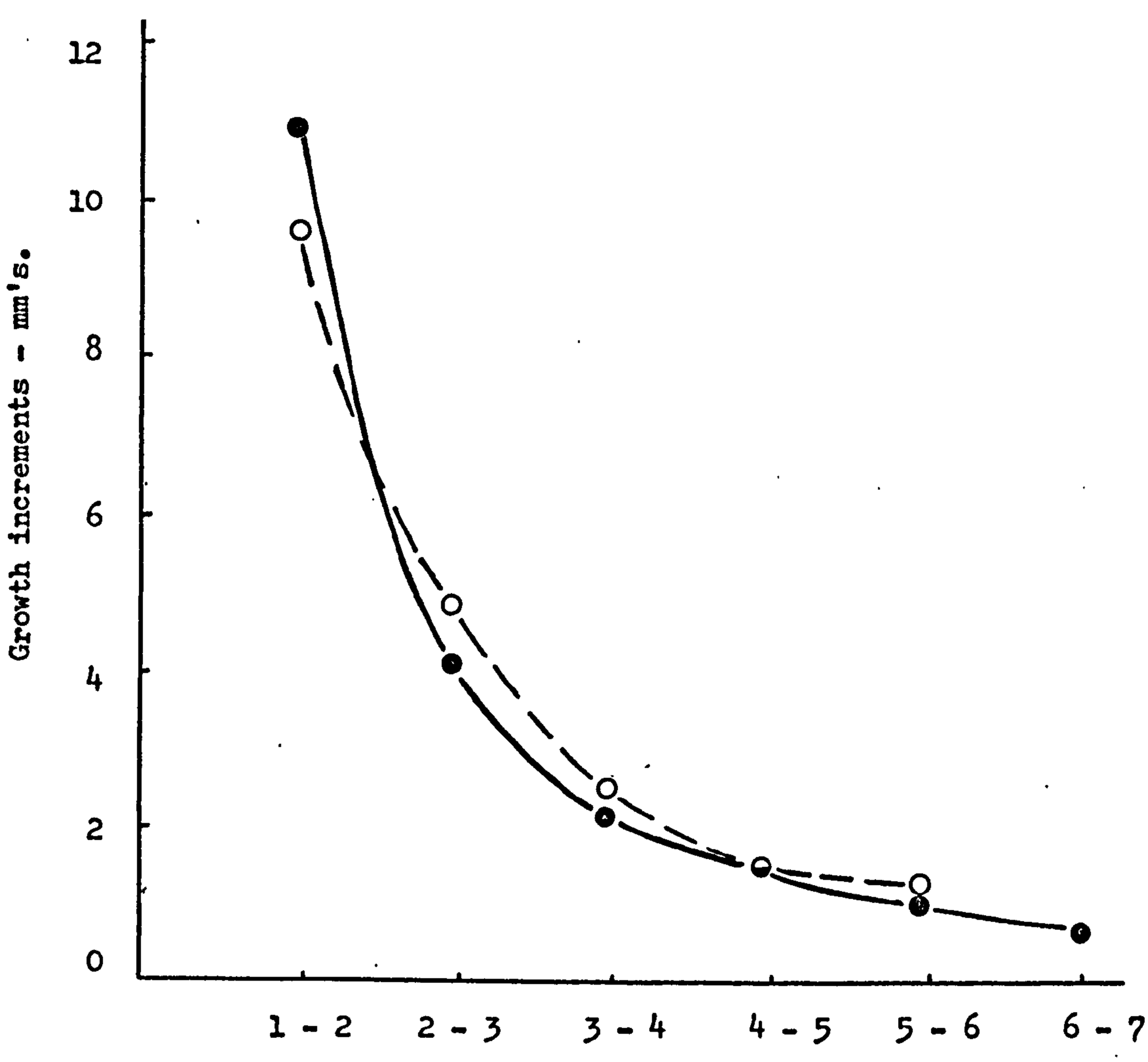


Fig 5 - Relative growth of the Cerastoderma from the Crouch mixed cockle population, determined by measurement of the increments added to the shell length each year.

●——● - C.edule.

○— —○ - C.glaucum.

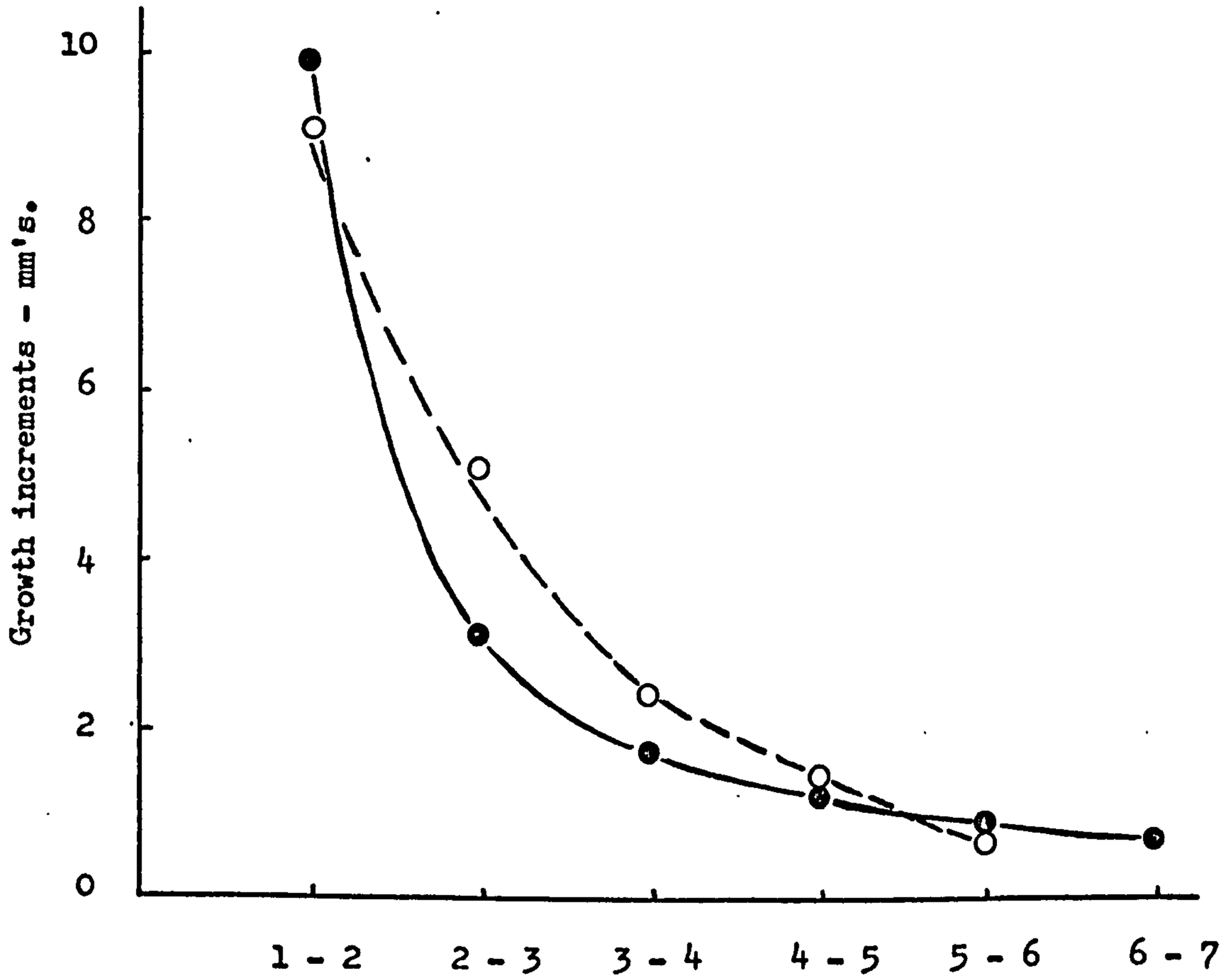


Fig 6 - Relative growth of the two Cerastoderma from the Crouch mixed cockle population, determined by measurement of the increments added to the shell depth each year.

●—● - C.edule.

o--o - C.glaucum.

consists of fast-growing, late settled individuals and slow-growing early settlers." Subsequent growth differs in the two groups, those which added the largest increments in the first year grow the least in the second and following years, being overtaken by those whose initial growth was slow but whose growth rate in the second and succeeding years is rapid. It seems that the growth rate of C.glaucum only overtakes C.edule in the third summer season, during the second to third year growth period. Thus, the growth of C.glaucum does not have the same characteristics as that of homogeneous C.edule populations that settle late in the season.

From tables 1 and 2 it is evident that a large growth increment, which may occur in a favourable growing season, can be detected in different aged cockles. Thus a good growing season in the summer of 1964 is reflected in the second year growth (1st to 2nd ring) of five year cockles, the third year growth of six year old individuals, and the fourth years growth of seven year cockles. The poor growing year of the 1967 summer is similarly reflected throughout the cockles growth increments.

Thus in conclusion, ~~although~~ the age structure of the two cockles from the mixed population is very similar, but for any given age C.glaucum tends to be 4-6.5 mm. smaller than C.edule. This is a reflection of the later spawning of C.glaucum which in the Crouch mixed cockle population occured on average seven weeks after C.edule (see Section VI). The growth rates of the two cockles have been shown to be very similar.

2. Shore distribution of the two members of the Cerastoderma

A transect was taken on 12.9.68 on a section of foreshore in the Crouch estuary some three kilometers downstream of Fullbridge ferry. This population was selected because of its isolation. (For location of site see figure 1 - Field studies in south-east England - Section IV).

Samples (0.1 m^2) were taken ashore at metre intervals from low water mark (L.W.M.). The substrate to a depth of about 15 cms. was sieved in a 5 mm. mesh sieve and the cockles counted and averaged. The shore profile was obtained by means of a rule, plumb line and spirit level. The profile of the shore and the distribution of the main substratum types are shown in fig. 7.

Only cockles over one year old, (i.e. with one winter ring) which could be identified easily are included in this survey. The 1968 spat fall was poor in the Crouch estuary, only 48 O-ring cockles were located on the transect line. These were predominately in the first five metres (shore distance) from L.W.M. The maximum density of cockles occurred at four metres (shore distance) above L.W.M. where a density of 390/m^2 was recorded. At 22 metres (shore distance) above L.W.M. no cockles occurred. Thus it can be seen that in this locality the Cerastoderma were only found in the lower regions of the shore, extension towards Mid Tide Level (M.T.L.) is probably prevented by the unsuitability of the substratum.

The distribution of C.glaucum and C.edule along the transect line is shown in fig. 8. It can clearly be seen that C.glaucum is only found at the lowermost shore levels, whilst C.edule extends, at much the same density, from low water mark to some 16 metres (shore distance) upshore.

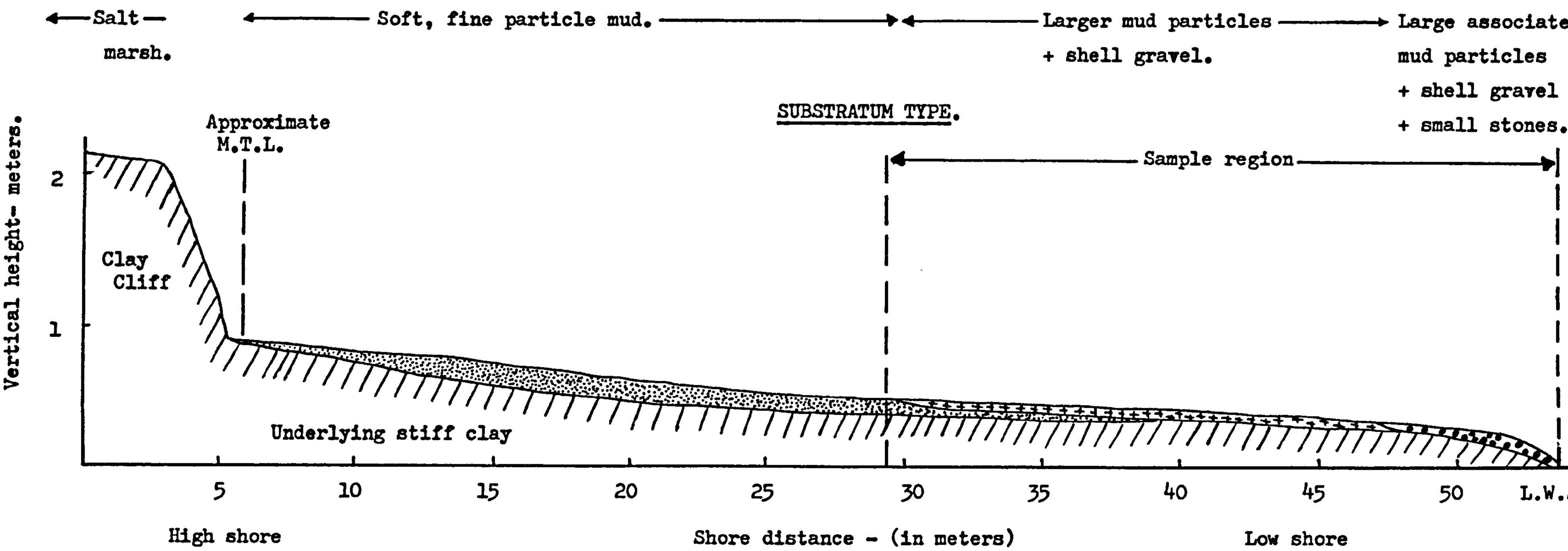


Fig 7 - Profile of the River Crouch estuary shore at the position of the transect.

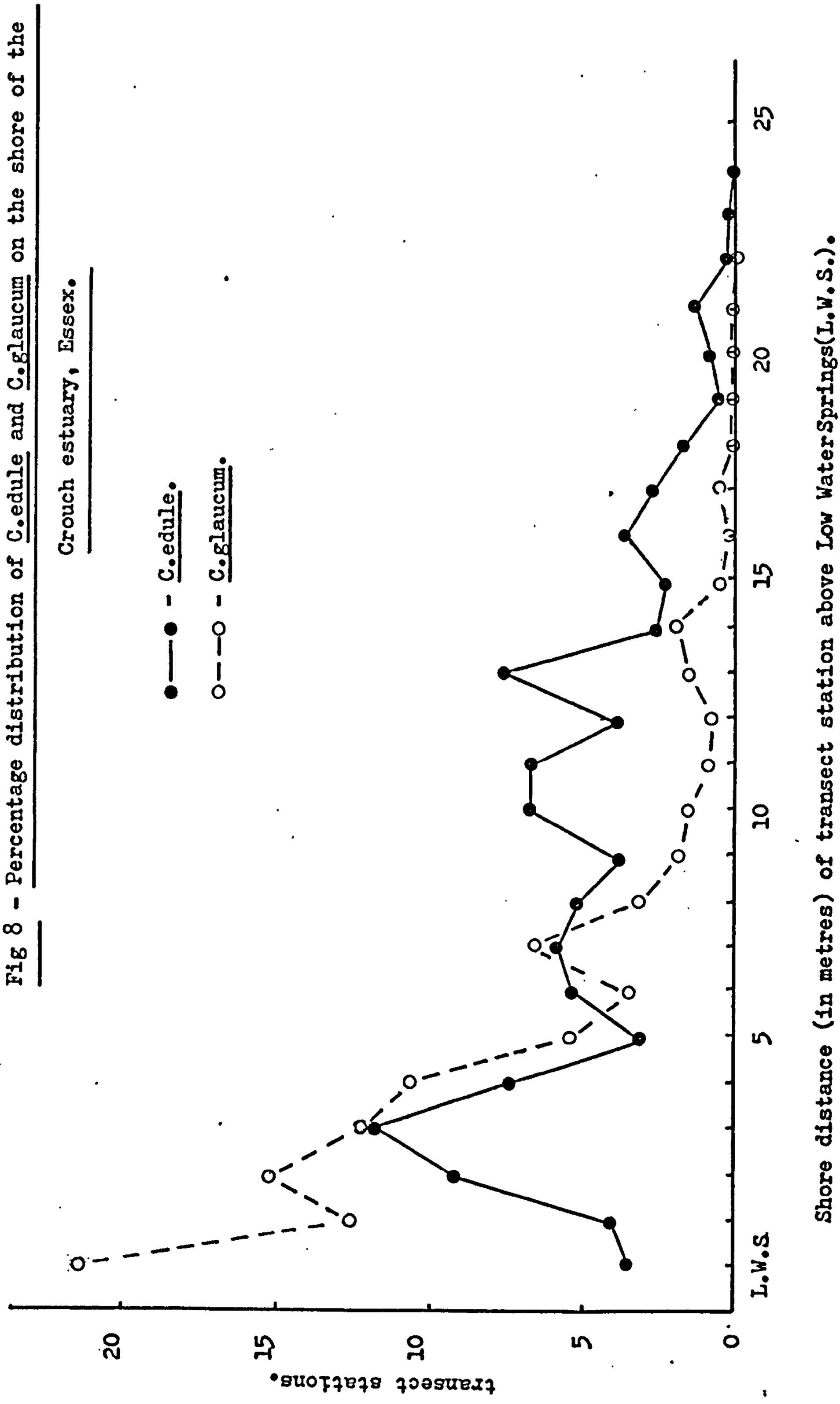


Fig 8 - Percentage distribution of C.edule and C.glaucum on the shore of the Crouch estuary, Essex.

●—● - C.edule.

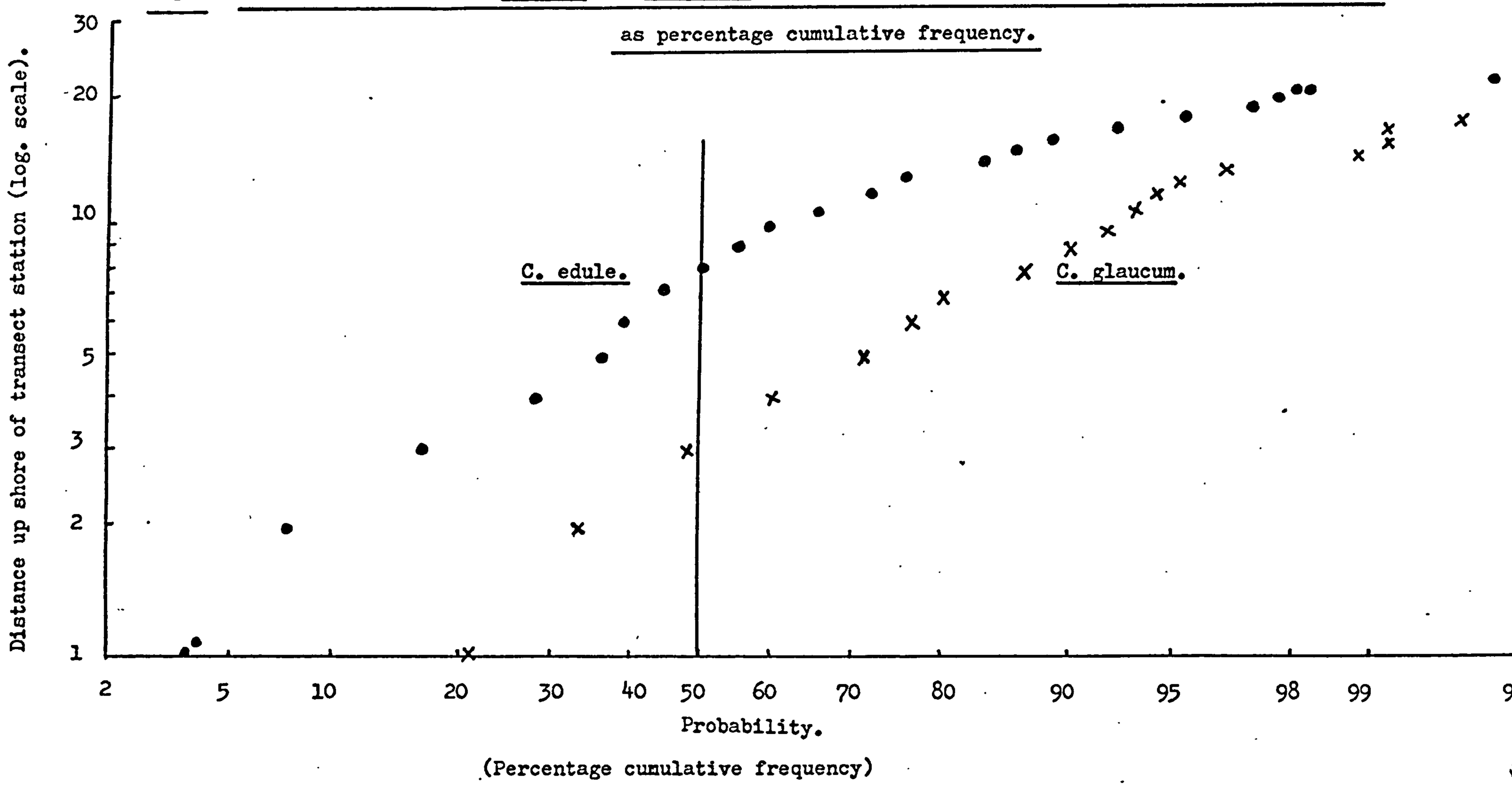
○—○ - C.glaucum.

This data plotted on log/probability paper as cumulative percentages is shown in fig. 9. 50% of the C.glaucum population occurred within three metres (shore distance) from M.W.N., whereas only 16% of the C.edule were found within this shore distance. C.edule has been found elsewhere in the Crouch estuary nearing M.T.L., thus it is unfortunate that it appears that substrate suitability for settlement, results at the level of the transect, in a restricted shore distribution for this cockle.

The occurrence of C.glaucum only at the lowest shore levels was to be expected from consideration of the ecology of single cockles populations discussed earlier, (see section IV). C.glaucum is typically found permanently submerged in non-tidal, stagnant, marine pools. (Boyden, 1969; Russell, 1963). It would seem therefore that the previous history of this cockle as a lagoon dweller, prevents the colonisation of higher shore levels when it re-invades a shore locality. It is possible that the tidal rhythms and behavioural responses exhibited by C.edule are absent in C.glaucum. Similarly, an inability to tolerate desiccation, high and low temperatures, may prevent C.glaucum from occupying high shore levels.

The shore distribution of C.edule varies depending upon the substrate suitability and the locality. Newell (1954) describing the marine fauna of Whitstable, Kent, records C.edule as occuring downshore from M.T.L., and a similar distribution was observed by Davis (1967) on the tidal flats of the Blackwater estuary, Essex. Kristensen (1956) working on the Dutch Waddensea flats, found the greatest concentration of cockles between M.T.L. and low water. However, Spooner and Moore (1940), in a study of the Tamar estuary, Devon, record C.edule as inhabiting all levels from High Water Neaps (H.W.N.) to the permanent river channel, with cockles most abundant between H.W.N. and M.T.L. Stephen (1953) reviewing his work on the distribution of lamellibranchs on Scottish sandy shores, reports C.edule

Fig 9 - Shore distribution of C.edule and C.glaucum in the Crouch estuary, plotted on probability paper as percentage cumulative frequency.



as occuring almost to H.W.N. in a C.edule - Macoma balthica zone stretching down the uppershore. In Poole Harbour, Dorset, Cole (1956), (quoting Green 1940) refers to cockles living at the level of H.W.N. among the roots of Spartina sp. As Poole experiences "double tides" each day it is possible that the occurrence of C.edule at high tidal levels at this locality is due to the exceptional tidal conditions. Finally, C.edule has been discovered on the western Eire coast at Shapletown living at high tidal levels, individuals only being covered for about 3½ hours every tide, and are therefore exposed to the air for approximately 17 hours out of 24.

Thus C.edule can occupy any tidal level up to H.W.N., but the shore distribution appears to be at least partly regulated by climate. On the east coast this cockle generally occurs below M.T.L., whereas in the west and north, it extends towards high water mark. It is interesting to note that where there is a low shore distribution, on the east coast, sub-littoral populations of C.edule also occur, e.g. Haplin Sands, Essex, The Wash and on various sub-littoral sand-banks in the North Sea (Kristensen, 1956).

3. Distribution of rib number in various cockle populations.

The family Cardiacea is characterised by the presence on the valves of the shells of prominent radial ribs running from the umbo to the valve margins.

One of the characteristics distinguishing C.lamarcki (=C.glaucum) from C.edule observed by Høpner - Petersen (1958), was the fact that the ribs on the posterior region of the shell of C.lamarcki were almost undeveloped. This feature had previously been noteddby Loppens (1923) in the "elongated form" of C.edule (=C.glaucum), and has subsequently been discussed by Elsma (1965) in C.edule var. lamarcki (also =C.glaucum). Mars (1951) in his review of the classification of the Cerastoderma, noted that typically C.edule from the Atlantic coasts had 24-26 ribs, whilst a range of 20-23 was found in C.glaucum from the Mediterranean.

As Eisma regarded rib number to be directly related to salinity, or some factor associated with salinity, it is of interest that Mars finds a low rib number in C. glaucum, even from the more saline Mediterranean. It is emphasized here that Eisma (1965) supported the theory that 'lamarcki' was a variety of C. edule.

Thus in the literature there is some confusion concerning the relationship of shell ribbing, salinity of environment and systematic status of the two cockles.

An investigation into the relationship of shell ribbing to salinity has been conducted in the British Cerastoderma, and compared wherever possible with the work of Eisma (1965) who reviews the previous work on rib-number in the Cerastoderma. Single Cerastoderma populations, which exhibit habitat isolation, have been studied, together with several mixed cockle populations.

(a) Measurement of rib-number

Cockle shells were cleaned to remove mud and algae which often obscure the ribs at the anterior and posterior shell margins. Live cockles were examined and in all cases the salinity of the environment has been determined, or obtained from another source. It has previously been shown by Walton (1919) and George (1924), that in C. edule greater than 0.98 cm. long, the rib number does not alter with age. Thus in this study the effect of age differences was ignored and a range of cockle sizes, from one to six year old individuals, were examined. It has also been shown by Purchon (1939) that the average rib number is not statistically different in littoral and sub-littoral populations of C. edule. Thus, although samples in this study came mainly from limited areas near low water mark, shore level was not regarded as critical.

It was found by Jayaker (1962) that the right shell valve of C. edule invariably had one more rib than the left, whilst Slijper (1926-9) records the reverse situation as more common. To prevent bias, only the ribs on

the left valve of each specimen were counted. Occasionally 'double ribs' occurred where two ribs had fused to create a single broad rib. In these rare circumstances a double rib was considered as two ribs.

(b) Factors affecting rib-number

The first appearance of ribbing on the young spat of C. edule occurs when the shell is about 1,400 μ long, (Benthem Jutting, 1943). Metamorphosis occurs some four to five weeks after spawning, in about Mid-June, Lebour (1938); and therefore, wherever possible, salinities have been determined for early summer when the process of rib-formation is taking place. If salinity or some other closely related environmental factor is regulating cockle shell rib number then it is at this time that it will be effective.

It has been suggested by Jayaker (1962) that substrate may be important in determining rib number, whilst previously Purchon (1939) observed that the cockle from marine sands have higher mean rib-numbers than those from estuarine muds. Certainly Eisma (1965) correlates rib-number with salinity, but he does not preclude the influence of some other factor of the environment associated with salinity.

(c) The effect of substrate upon rib-number

A section of foreshore at Southend along the North Thames coast was selected, which exhibited a wide range of substrate types, from soft mud, (fine particle size), to muddy-sand (basically sandy but with some smaller particles present), but where the salinity remained roughly constant. The first locality was at Chalkwell Coze, the second, adjacent to the boom at Shoeburyness. The amount of wave action and tidal scour is also greater at this latter locality. The salinity varies very little over this region of some seven miles, at high tide the values obtained in the summer of 1970 being 28.7‰ at Shoeburyness and 27.4‰ at Chalkwell.

100 C. edule were collected from each of the two localities on 6.3.68. and the number of ribs counted. The results can be seen in fig. 10 and table 4. Clearly neither the mean or the range of rib-numbers differ from these two sites. It is unlikely that settling spat are moved large distances, especially from the very fine substratum locality at Chalkwell, to obtain uniformly distributed spat over the seven miles. Thus it would appear that the type of substrate has no direct effect upon the number of ribs exhibited upon the cockle shell.

(d) Distribution of rib-numbers in the Crouch and Roach mixed cockle populations.

The rib numbers of a sample of 520 cockles collected in May 1968 from the Crouch mixed population were counted and the resulting distribution is shown in fig. 11. The data was then converted to cumulative percentages, see table 5, and plotted on probability paper, fig. 12. It is evident considering this latter figure, that the apparently near normal distribution displayed in fig. 11 is in fact a composite of two overlapping normal distributions. This is deduced, as two straight lines can be fitted to the tail sections of the curve of cumulative percentage/probability distribution, indicating a bimodal form. (For a recent application of arithmetric probability paper to a biological system, separating polymodal frequency distributions, see Harris, 1968).

The cockle sample was then divided into the two Cerastoderma types, C. edule and C. glaucum. On plotting the distribution of rib-numbers, two separate normal distributions resulted. The histograms obtained are shown in figs. 13 and 14. Calculating as cumulative percentages for each cockle type, (see table 5) and plotting as above, fig. 15, results in two straight lines, emphasizing the normality of these rib number distributions. A similar phenomenon was found in the Roach estuary cockles, and the

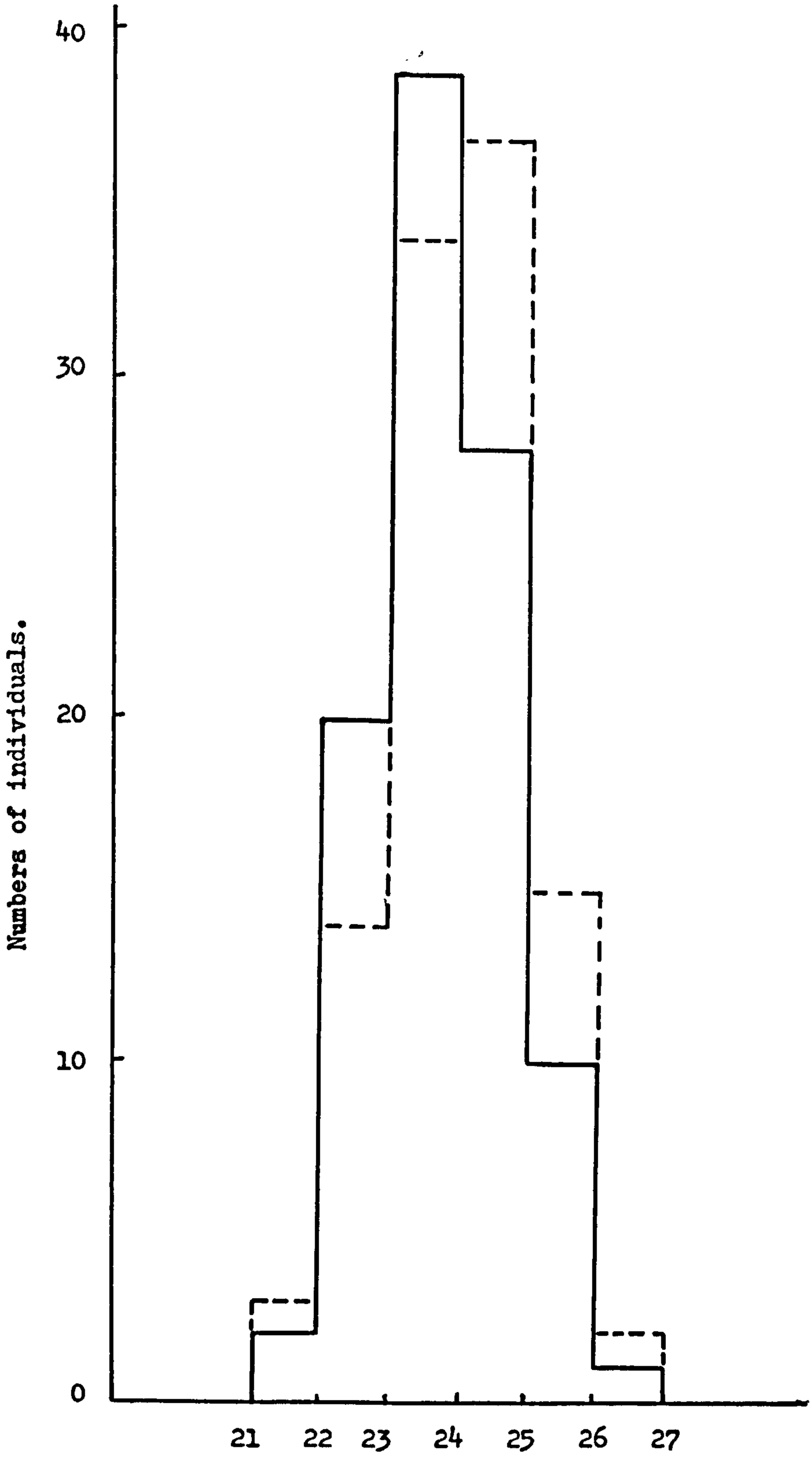


Fig 10 - Distribution of rib-number in two C.edule populations from the Southend area, Essex.

——— = cockles from Chalkwell (fine mud habitat.)

– – – – = cockles from Shoeburyness (muddy - sand habitat.)

Table 4

Statistical comparison of rib- number distribution in two C. edule populations from Southend, Essex.

Statistical Character.	Chalkwell population.	Shoebury population.
Number in sample - n	100	100
Range of rib-number	22 - 27	22 - 27
Mean rib-number - $\bar{x}$	24.28	24.55
Standard error of mean- $\frac{S.D}{\sqrt{n}}$	$\pm$ 0.1010	$\pm$ 0.1027
Estimate of variance of mean- s^2	1.0198	1.0550
" " " " S. D. - s	1.010	1.027

Equality of the two variances

F - test - $\frac{s_1^2}{s_2^2}$ - 1.035

(Therefore not significantly different)

Significance of difference between two sample means -

$$s_x^2 = \frac{(n_1 - 1)s^2 + (n_2 - 1)s^2}{n_1 + n_2 - 2}$$

t - test :

$$t = \frac{\bar{x}_1 - \bar{x}_2}{s_x\sqrt{\frac{1}{n_1} \quad \frac{1}{n_2}}} = 1.875$$

Therefore difference between rib-number in the above populations of C.edule are not significant at the 5% level.

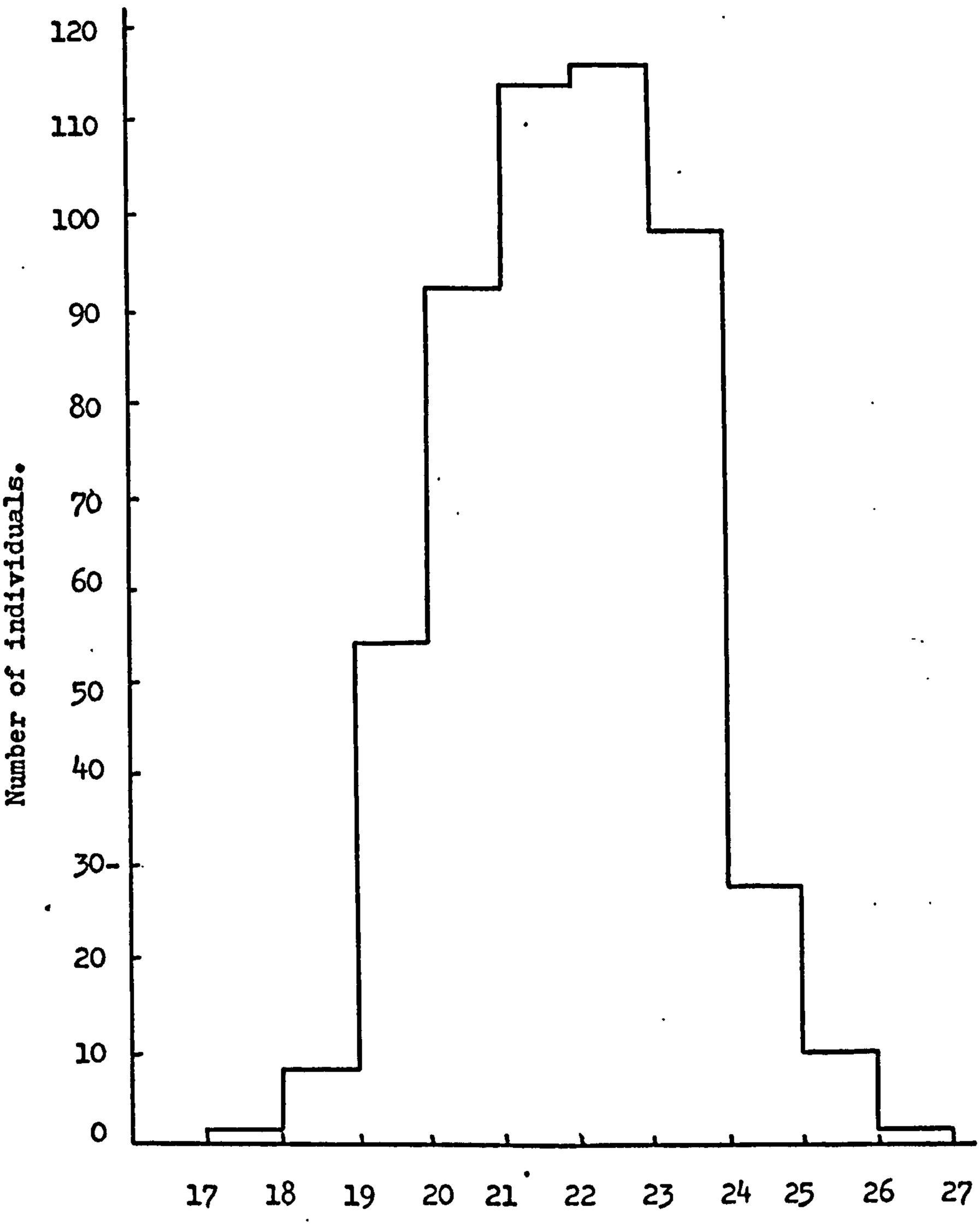


Fig 11 - Distribution of rib-numbers in cockles from the Crouch mixed population.

(combined graph: 260 C.edule and C.glaucum).

Mean rib-number= 21.40

Table- 5a)

Cumulative data of rib- number in cockles collected from the Crouch population, to indicate the presence of two superimposed normal distributions.

Data then plotted on Probability paper.

Abscissa- Rib-number.	Number of cockles with each rib-number.	Cumulative ordinate.	%age cumulative ordinate.
18	1	1	0.193
19	6	7	1.351
20	54	61	11.776
21	92	153	29.537
22	114	267	51.544
23	115	382	73.745
24	98	480	92.664
25	28	508	98.069
26	9	517	99.807
27	1	518	100.000

Table- 5b)

Comparison of two normal distributions of rib-number in C.edule and C.glaucum from the Crouch mixed population.

-Tabulation of data for analysis on Probability paper.

Abscissa- Rib-number.	Ordinate-nos. of C.edule.	Cumulative Ordinate.	%-cumulative ordinate.	Ordinate C.glaucum	Cumulative Ordinate.	%-cumulative ordinate.
18	-	-	-	1	1	0.388
19	-	-	-	6	7	2.692
20	2	2	0.769	52	59	22.692
21	12	14	5.385	80	139	53.876
22	40	54	20.769	74	213	82.558
23	79	133	51.115	36	249	96.512
24	91	224	86.154	7	256	99.225
25	26	250	96.154	2	258	100.000
26	9	259	99.615	-	-	-
27	1	260	100.000	-	-	-

Table - 5c)

Comparison of two normal distribution of rib - number in C.edule and C.glaucum from the Roach mixed population.

Tabulation of data for analysis on probability paper.

Abscissa Rib-number	Ordinate-nos. of C.edule	Cumulative Ordinate.	%-cumulative ordinate.	Ordinate C.glaucum	Cumulative Ordinate.	%-cumulative ordinate.
18	-	-	-	1	1	1.124
19	-	-	-	3	4	4.494
20	-	-	-	15	19	21.348
21	1	1	1.064	28	47	52.809
22	16	17	18.085	22	69	77.528
23	23	40	42.553	14	83	93.258
24	30	70	74.468	5	88	98.876
25	13	83	88.298	1	89	100.000
26	9	92	97.872	-	-	-
27	2	94	100.000	-	-	-

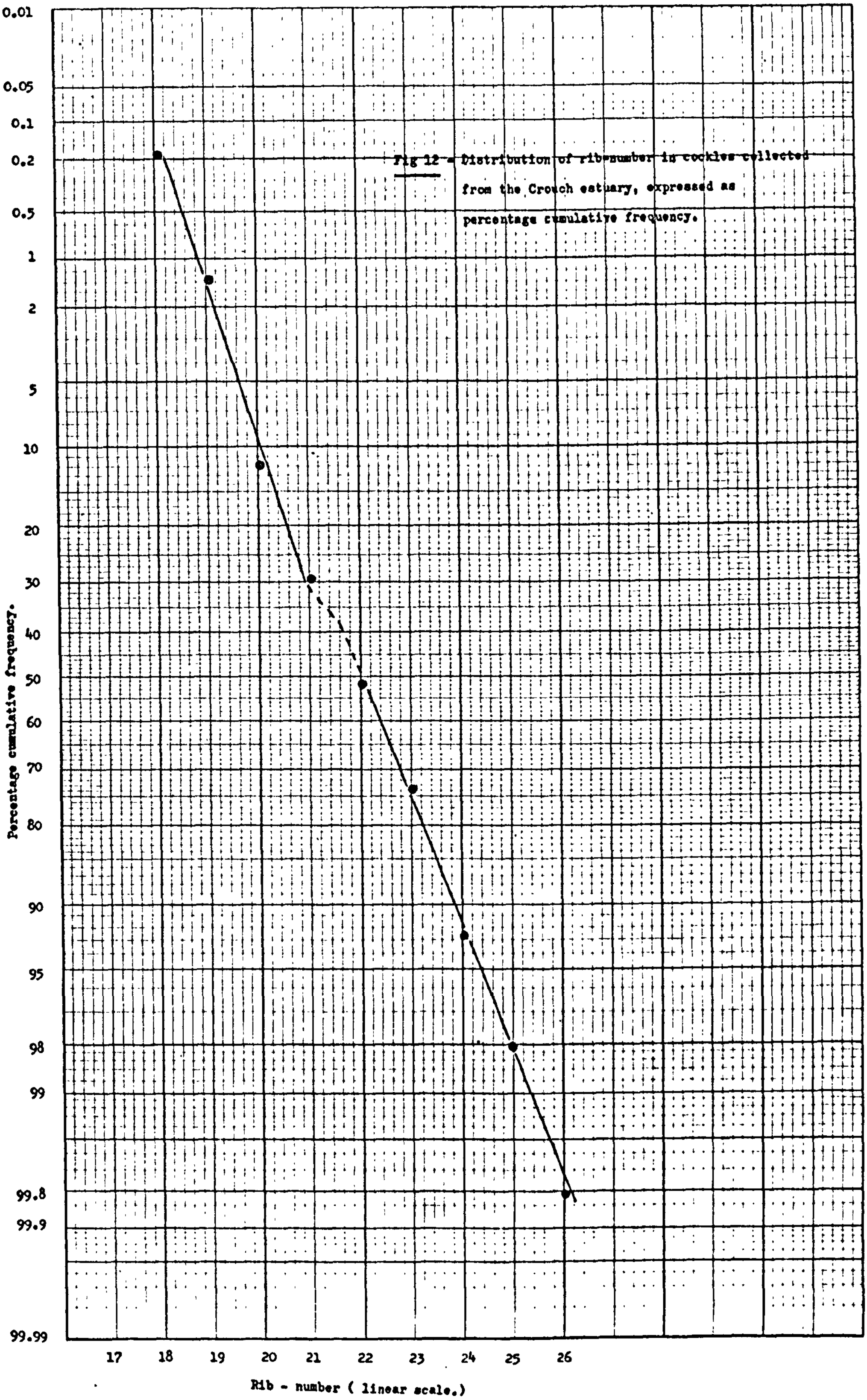


Fig 12 - Distribution of rib-number in cockles collected from the Crouch estuary, expressed as percentage cumulative frequency.

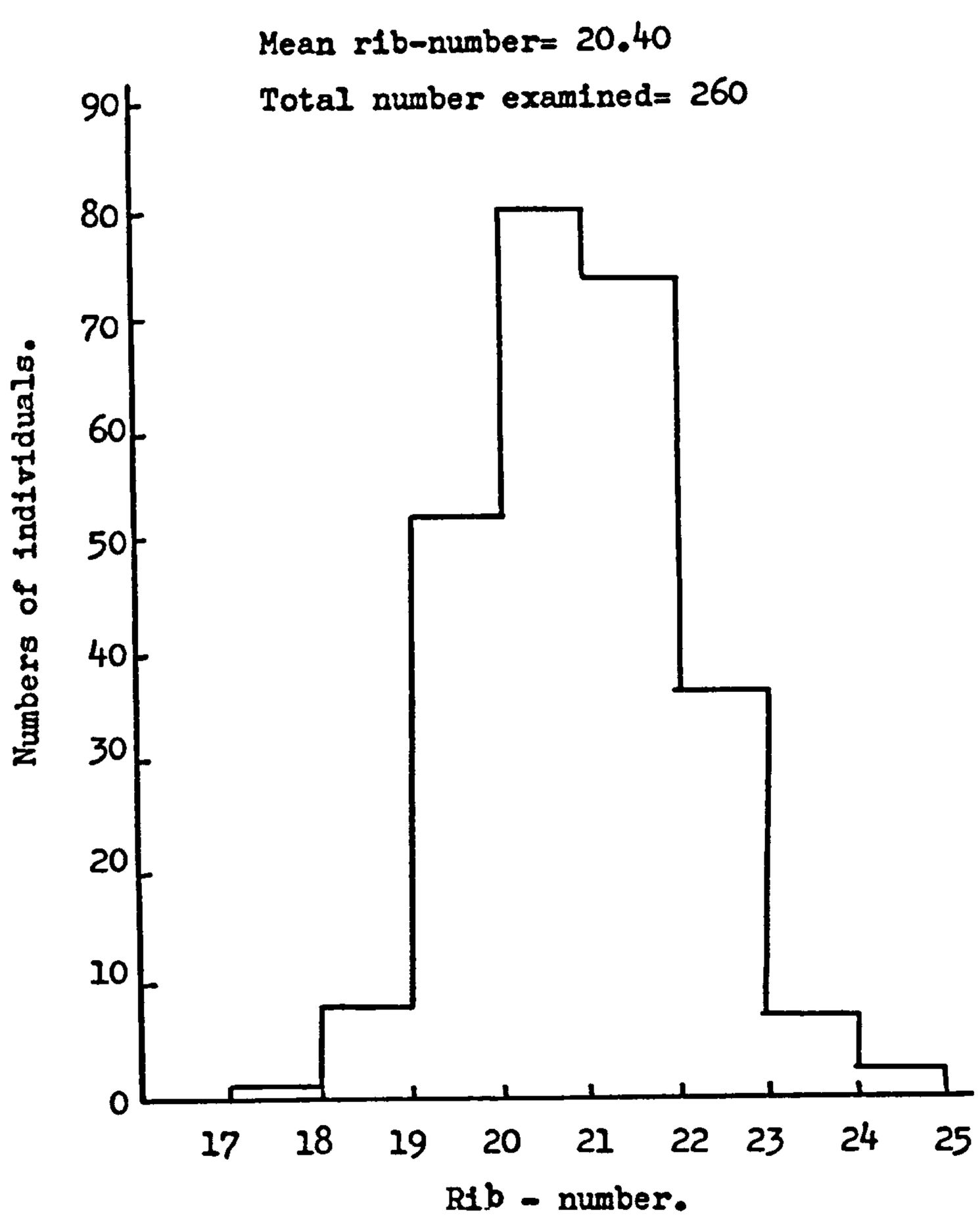


Fig 13 - Distribution of rib-number in C.glaucum from the Crouch mixed population.

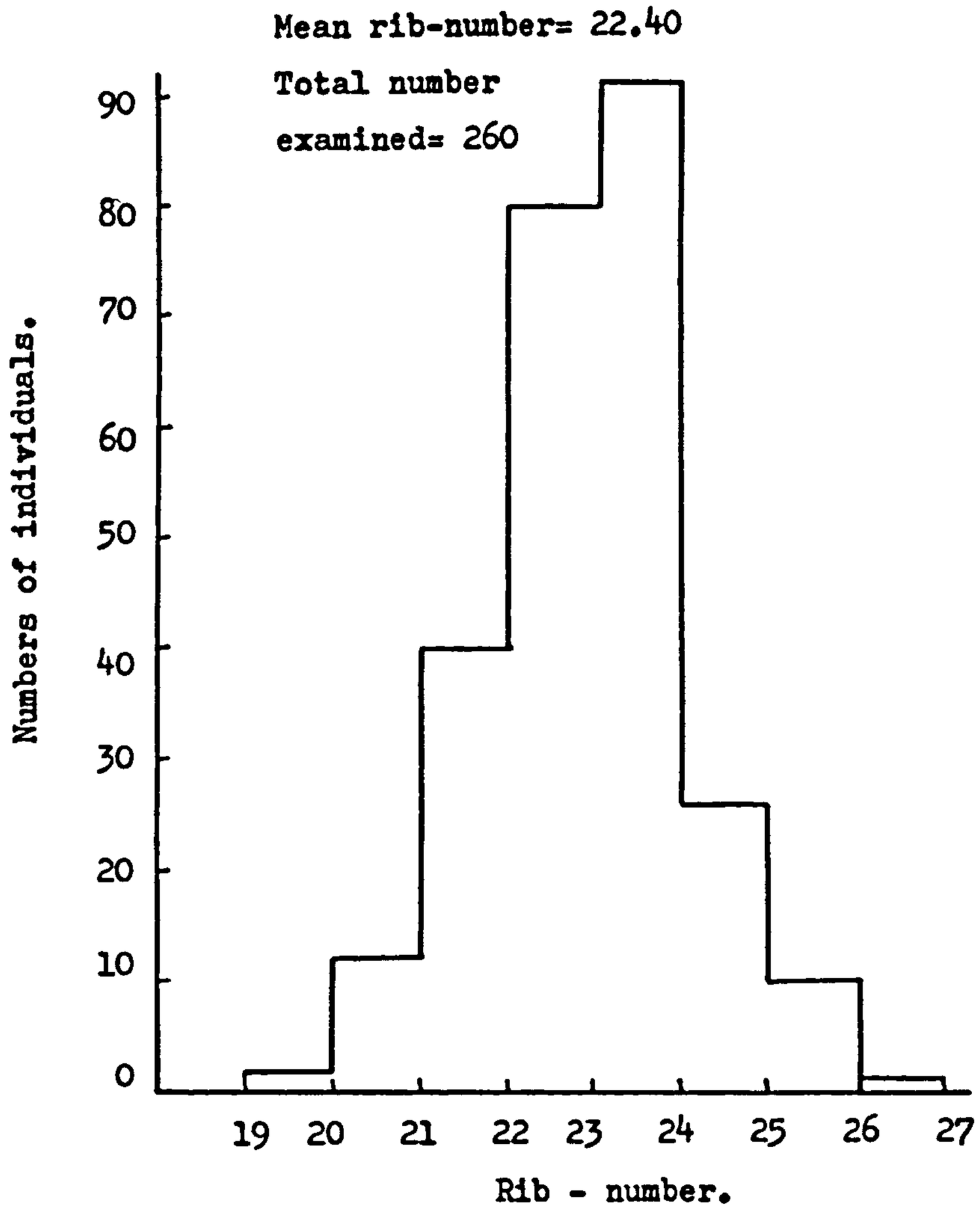


Fig 14 - Distribution of rib-number in C.edule from the Crouch mixed population.

distributions of the single cockle types have been included in fig. 15.

Thus in the mixed cockle populations, the distribution of rib number is normal in the two cockle types, and the two distributions are separable using probability paper. It would also seem that in the estuarine environments of the Crouch and Roach, Essex that the average rib number of C. glaucum is less than in C. edule. For statistical analysis of rib number data see table 6.

The mean rib numbers for other mixed populations of the Cerastoderma are shown in table 7, and thus the validity of this observation on the Crouch and Roach cockles is borne out elsewhere in the British Isles. This feature of reduced rib number in C. glaucum compared with C. edule is in direct contrast to the views of Eisma (1965), who was unable to find any differences in the rib number of the two cockles from a mixed community. Moreover, the results obtained here have been substantiated by Russell (1969), who considered the same Roach estuary sample, and also several Danish localities. It would seem therefore that there is a genetic component involved with rib number determination.

(e) Distribution of rib-number in single cockle populations

The histogram distribution patterns of rib-number from several single cockle populations are displayed in fig. 16. It can be seen that , in general, the variation in rib-number of littoral C. edule populations is less than that found in lagoon populations of C. glaucum. The 'tails' of the normal distribution of rib numbers in C. glaucum are extended to cover a greater range and give the distribution a more flattened appearance. However, taking into consideration all the populations examined, the total range of rib number from 18 - 30 appears to be no different in the two cockle types. Within lagoons during the limited period of rib number determination at metamorphosis, the salinity is likely to remain fairly

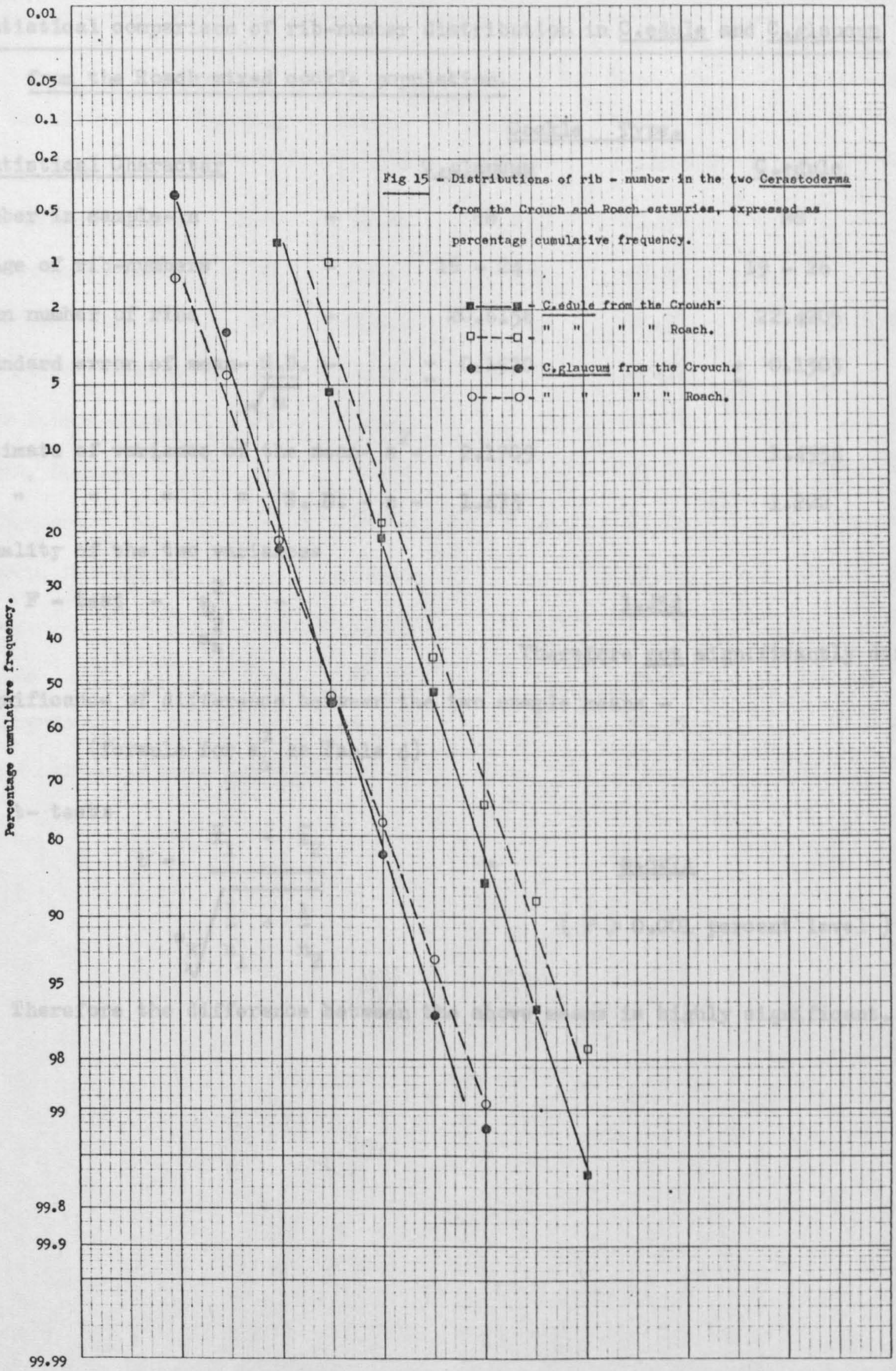


Fig 15 - Distributions of rib - number in the two Cerastoderma from the Crouch and Roach estuaries, expressed as percentage cumulative frequency.

Table 6

Statistical comparison of rib-number distribution in C.edule and C.glaucum from the Roach mixed cockle population.

Statistical Character	Cockle Type. C.glaucum	C.edule
Number in sample- n -	88	88
Range of rib-numbers -	16 - 24	19 - 26
Mean number of ribs -	20.6136	22.4205
Standard error of mean- $\frac{S.D.}{\sqrt{n}}$ -	$\pm$ 0.1570	$\pm$ 0.1303
Estimate of variance of the mean- s^2 -	2.1709	1.4934
" " " " S. D. - s -	1.473	1.222

Equality of the two variances

F - test - $\frac{s_1^2}{s_2^2}$ - 1.454

Therefore not significantly different

Significance of difference between the two sample means -

(formula for s_x^2 as Table 4)

t- test:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{s_x\sqrt{\frac{1}{n_1} + \frac{1}{n_2}}} = 8.8271$$

(P > 0.001 percent level)

Therefore the difference between the above means is highly significant.

Table 7

Comparison of rib-number between C.edule and C.glaucum from mixed populations.

Locality.	Number of C.edule examined.	Mean rib number of C.edule.	Number of C.glaucum examined.	Mean rib number of C.glaucum.	Estimated summer salinity of environment.
Crouch estuary-Essex	260	22.40	260	21.40	
Roach estuary- Essex	88	22.42	88	20.61	
Chaptetown, Eire	40	23.60	18	20.92	33.2 %
Poole Harbour-Dorset	17	23.47	8	20.37	
Horsey Island-Hants.	23	24.26	3	(22)	32.5 %
Pughavn, Denmark *	-	24.04	-	23.28	19.5 %
Oro, Denmark *	-	24.62	-	23.04	15.7 %
Vellurup, Denmark *	-	24.10	-	22.60	16.0 %
Nkobing, " *	-	23.75	-	22.04	16.2 %
Roskilde " *	-	23.75	-	23.12	16.0 %
Jaegerspris " *	-	24.25	-	22.91	15.0 %

* (Data extracted from Russell(1969).)

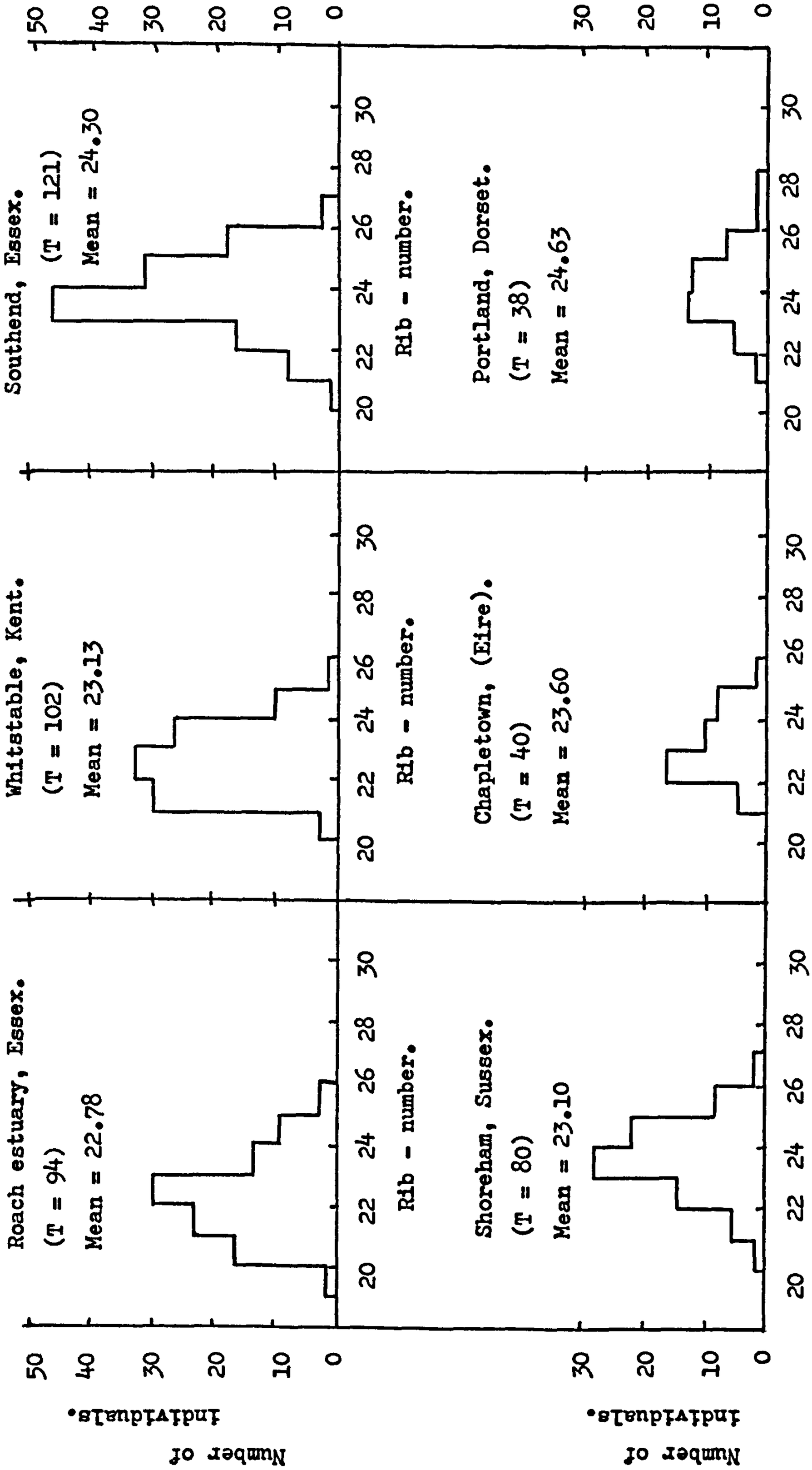


Fig - 16 (A) - Distribution of rib-number in various shore populations of C.edule.

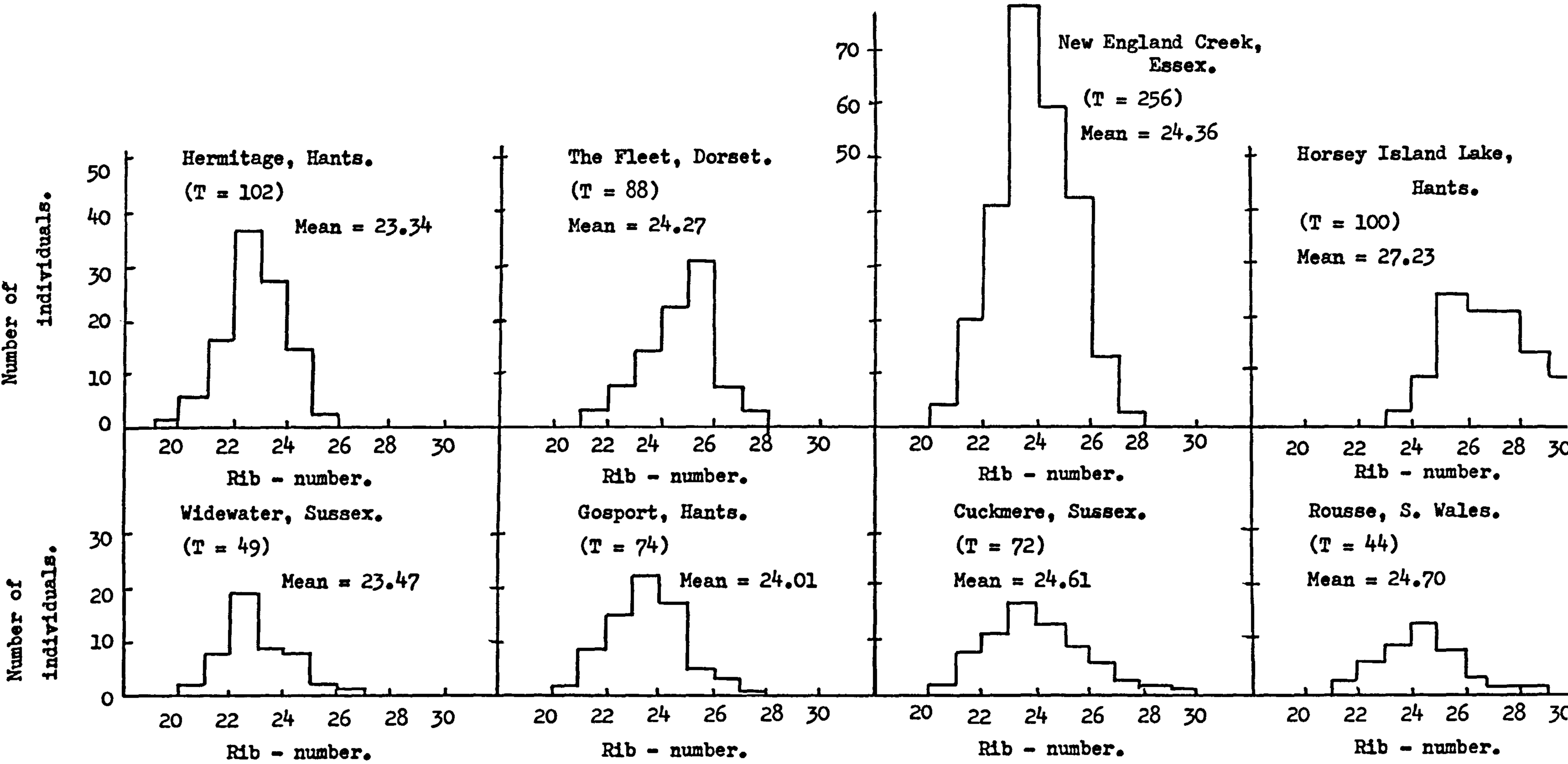


Fig 16 (B) - Distribution of rib-number in various populations of lagoon C.glaucum.

constant. However, in the cockles from these localities there is a wide range of rib numbers which may indicate a certain amount of genetic control over rib number, or the importance of other environmental parameters upon rib number.

In this study, in contrast to Eisma (1965), differentiation between C. edule and C. glaucum has been recognised as important when considering the relationship of rib number to the environment. Amalgamating samples of the two cockles from environments with apparently similar salinity regimes, (as Eisma, 1965), may mask the separate reactions of the two cockles to that parameter. Thus the complex nature of the relationship of mean rib-number to salinity as compiled by Eisma, (reproduced in fig.17) may be due to the non-homeogenity of the cockle samples used.

(f) Relationship of rib number to salinity in single cockle populations.

(i) Cerastoderma edule

Early studies upon ribbing of cockle shells dealt almost solely with C. edule - (Walton, 1919; George, 1924; Purchon, 1939; Jayaker, 1962). Thus in the literature observations on average rib numbers for various C. edule populations are available. Eisma (1965) considered many different populations from Europe and has tabulated most of the available information. From his excellent tables the average rib number of single cockle populations of C. edule and C. glaucum have been extracted.

As was pointed out earlier, salinity, or some other factor associated with salinity, has been considered to be an important element regulating cockle rib number. However, salinity is a very variable environmental parameter, especially in estuaries and lagoons where the Cerastoderma commonly occur, altering both seasonally and tidally.

The information from various authorities is shown in table 8, and the relationship of mean rib number (M.R.N.) to salinity for C. edule has been graphed in fig. 18.

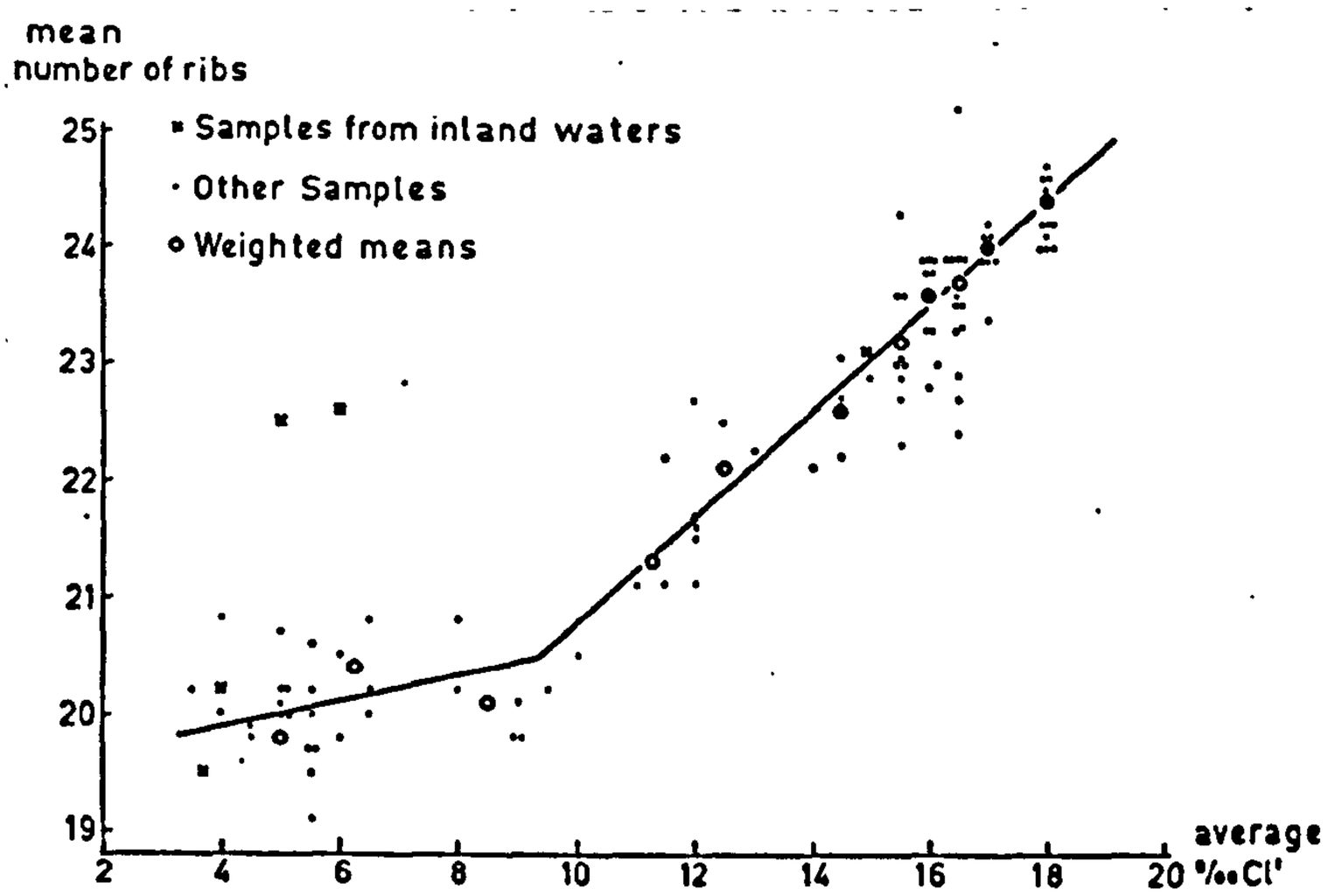


Fig 17 - Relationship between average number of ribs and average chlorinity for samples of cockles from Dutch coastal waters. (From Eisma(1965))

Table 8

Locality.	Numbers of cockles in sample.	Range of rib numbers.	Mean rib number.	Estimated summer salinity of environment.
Portland, Dorset.	38	(22-28)	24.63	34.5 ‰
Southend, Essex.	321	(22-27)	24.36	31.0 ‰
Portsmouth, Hants.	23	(21-27)	24.26	32.5 ‰
Chapletown, Eire.	40	(22-26)	23.60	33.2 ‰
Poole Harbour, Dorset.	17	(22-26)	23.47	32.3 ‰
Whitstable, Kent.	102	(21-26)	23.13	32.8 ‰
Shoreham, Sussex.	80	(21-27)	23.10	32.5 ‰
Roach estuary, Essex.	88	(19-26)	22.42	31.0 ‰
Crouch estuary, Essex.	260	(20-27)	22.40	30.8 ‰

From other authorities:

Locality.	Numbers of cockles in sample.	Range of rib numbers.	Mean rib number.	Estimated salinity.*
Roscoff, France. [1]	73	-	26.50	34.7 ‰
St. Efflam, France. [1]	607	-	25.90	34.7 ‰
Setubal, Portugal. [2]	13	-	26.30	36.5 ‰
Agadir, Morocco. [2]	12	-	25.80	36.5 ‰
Stavanger, Norway. [2]	14	-	24.70	32.7 ‰
Luc sur Mer, France. [3]	1600	-	24.40	32.7 ‰
Boulogne, France. [3]	575	-	24.20	32.7 ‰
Pughavn, Denmark. [4]	-	-	23.70	19.5 ‰
Swansea Bay, S. Wales. [5]	1000	(22-29)	25.60	c.30.0 ‰
Millport, Scotland. [6]	50	(23-27)	25.24	c.32.7 ‰
Pier Cellars, Plymouth. [6]	50	(21-26)	24.01	c.32.0 ‰
St. John's Lake, Plymouth. [6]	50	(18-25)	21.40	c.32.0 ‰
Bardsea, Morecambe, Lancs. [7]	300	(20-27)	23.46	c.32.0 ‰
Penclawdd, S. Wales. [3]	1006	-	24.20	c.32.0 ‰
Near Exmouth, Devon. [8]	100	(20-28)	23.80	c.32.0 ‰
Exe estuary, Devon. [8]	100	(20-26)	23.13	c.32.0 ‰

* -(Chlorinity figures of Eisma(1965) converted to salinity.)

Authorities:

1 - Jayakar(1962)
2 - Eisma(1965)
3 - Slijper(1926-29)
4 - Russell(1969)
5 - George(1924)
6 - Purchon(1939)
7 - Walton(1919)
8 - Loppens(1923)

Table 8 (continued)

Locality.	Number of cockles in sample.	Mean rib number.	Salinity of environment. (converted from values of Eisma, 1965.)
Wadden Sea.			
Zuidwal dijk-A6 and Omdraai	98	23.6	29.2 ‰
Bank 't Kuitze and Zeehondenplaat	69	23.9	30.0 ‰
Staart van Schieringhals	51	24.11	31.0 ‰
Eyerlandse Gat	10	24.2	32.0 ‰
Rhine- Meuse- Scheldt estuary.			
Kruiningen veer	21	22.2	21.0 ‰
Biezelugse Ham	17	22.5	22.8 ‰
Philippine	22	23.1	26.5 ‰
Kaloot	30	23.0	28.4 ‰
Nw . en St. Joosland & kitthem	100	22.6	27.4 ‰
Vlissingen & Vlissingen Strand	78	23.3	29.2 ‰
Nieuwvliet	37	23.6	31.0 ‰
Dishock and Zoutelande	48	23.3	30.0 ‰
Eastern Scheldt.			
Krabbekreek	100	23.6	28.4 ‰
Colijnsplaat	50	23.6	30.0 ‰
Bank Onrust and Domburg Strand	31	24.1	32.0 ‰
Grevelingen.			
Brouwershaven and Goeree	66	22.7	28.4 ‰
Haamstede and N.W.Voorne Strand	59	24.0	31.0 ‰

All the above Netherland localities have been extracted from Eisma (1965). Samples containing only C.edule have been considered, all those stated to contain a percentage of C.edule var lamarcki (= glaucum) have been discarded.

There is a direct relationship between M.R.N. and salinity in C. edule, with a progressive increase of rib number in the salinity range 19 - 33‰. It is however pointed out, that the lower salinity environments tend to be sheltered estuaries, whilst the highest salinity sites are relatively exposed, marine sands. It may be that wave action, as suggested by Purchon (1939), which is often indirectly associated with salinity, is influencing to some extent the M.R.N.

(ii) Cerastoderma glaucum

The information available in the literature for C. glaucum is less detailed. The M.R.N. has been determined for populations of this cockle from various lagoon localities around the British Isles. Data has been extracted from Eisma (1965) for inland waters of the Netherlands and for several Mediterranean localities. The data of Eisma on C. edule var lamarcki (= C. glaucum) from the former Zuiderzee, Holland, ~~have~~ has been excluded, as in these samples preserved material was studied and average salinities of the environments deduced not measured.

The available data is shown in table 9 and the relationship of M.R.N. to salinity is expressed in fig. 19. It can be seen that single populations of C. glaucum exhibit low rib-numbers in low salinity waters, rising to a maximum in environments between 20-30‰, finally dropping again in waters higher than 35‰ salinity.

This trend fits the isolated information previously noted in the literature concerning cockle ribbing and environmental salinity. Thus the low average rib-number in C. glaucum from the Mediterranean compared with C. edule, recorded by Mars (1951) is explained by the fact that in high salinities, rib formation seems to be inhibited in C. glaucum. Similarly, it has long been known from the early observation of Bateson (1889) that C. edule (in reality C. glaucum) from the terraces surrounding the

Table 9

Relationship of Rib Number to Salinity in various populations of C.glaucum.

Locality, date and state of sample.		Numbers of cockles in sample.	Range of rib numbers.	Mean rib number.	Estimated summer salinity of environment.
1) Lagoons.					
Horsey Island Lake, Hants.		100	(24-30)	27.23	24.2 ‰
Roose, Nr. Barry, S. Wales.					
	-live 14. 3.68				
	-live 30. 7.69	17	(23-28)	25.35	21.4 ‰
	-dead "	44	(22-29)	24.70	
Brightlingsea, The Fleet, Dorset	-live 7. 5.68	30	(22-27)	25.07	20.3 ‰
-Langton Herring	-live 12. 8.68	88	(22-28)	25.15	29.2 ‰
-Wyke Regis	- " "	41	(22-27)	24.27	33.6 ‰
Cuckmere, Sussex	- " 14. 3.68	72	(21-30)	24.61	20.3 ‰
New England Creek	- " 28. 1.69	246	(21-28)	24.36	(25.3 ‰ - from Howes(1939))
Gosport, Hants.	- " 6. 6.69	80	(21-28)	24.01	28.2 ‰
Trawnagh, Eire.	- " 4. 8.69	18	(22-26)	23.94	26.25 ‰
	-dead "	15	(22-26)	23.93	
Widewater, Sussex	-live 14. 3.68	49	(21-27)	23.47	22.2 ‰
Hermitage, Hants.	- " 12. 5.68	102	(20-26)	23.34	10.4 ‰
Finavarra, Eire.	- " 4. 8.69	11	(22-25)	23.09	8.7 ‰
Sheerness, Kent.	- " 17. 6.69	44	(21-27)	23.68	16.0 ‰
Records from Eisma(1965) of other North European, inland saline pool localities:-					
Dreischor Dijkwater, Zeeland		50	-	22.6	11.1 ‰
Zierikzee	"	22	-	22.5	9.2 ‰
Groote Gat Oostburg	"	18	-	20.2	7.2 ‰
Petten, North Holland		43	-	19.5	6.8 ‰
2) Mediterranean					
Castellon	Eisma(1965)	16	-	24.0	37.4 ‰
Sète	"	12	-	23.2	37.4 ‰
Cavalaire	"	14	-	24.5	37.4 ‰
Porte Vecchio(Corsica)	Eisma(1965)	4	-	23.8	37.4 ‰
Haifa	"	7	-	23.3	38.25 ‰
El Coefica(Benghazi)					
	- Kaltenbach(1943)	34	-	24.1	38.25 ‰
Etang de Gloria	- Russell(1969)	- (live)	-	21.2	37.5 ‰

Table 9 (continued)

Relationship of Rib Number to Salinity in various populations of C.glaucum.

Locality.	Size of sample.	Authority	Mean rib number.	Salinity of environment.
3)Baltic Sea populations				
Jastania	24	Eisma(1965)	20.5	7.2 ‰
Rossiten	14	" "	19.4	7.2 ‰
Nrd. Oland	17	" "	20.9	7.2 ‰
Kammin (Pommern)	780	Slijper(1926-29)	20.2	7.2 ‰
Dantzig	670	"	20.1	7.2 ‰
4)Other populations of C.glaucum from Netherland localities				
Zuiderzee - Elburg	19	Eisma(1965)	20.2	6.25 ‰
Western Scheldt Estuary (-Nw. en St. Joosland)	16	" "	24.3	28.25 ‰
Eastern Scheldt, (-Arnemuiden)	41	" "	23.9	30.0 ‰

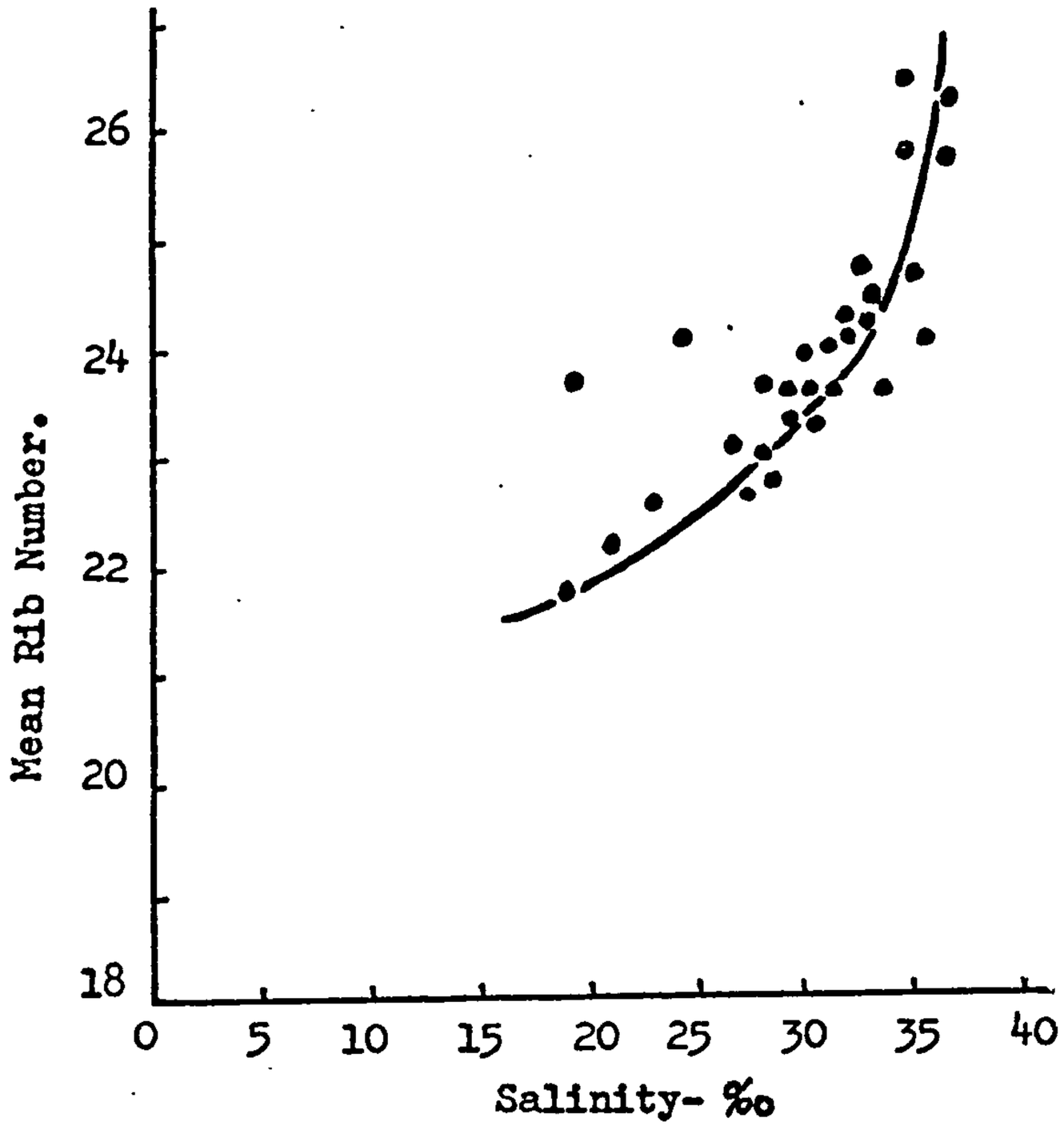


Fig 18 - Relationship of mean rib number to salinity in various littoral populations of C.edule.

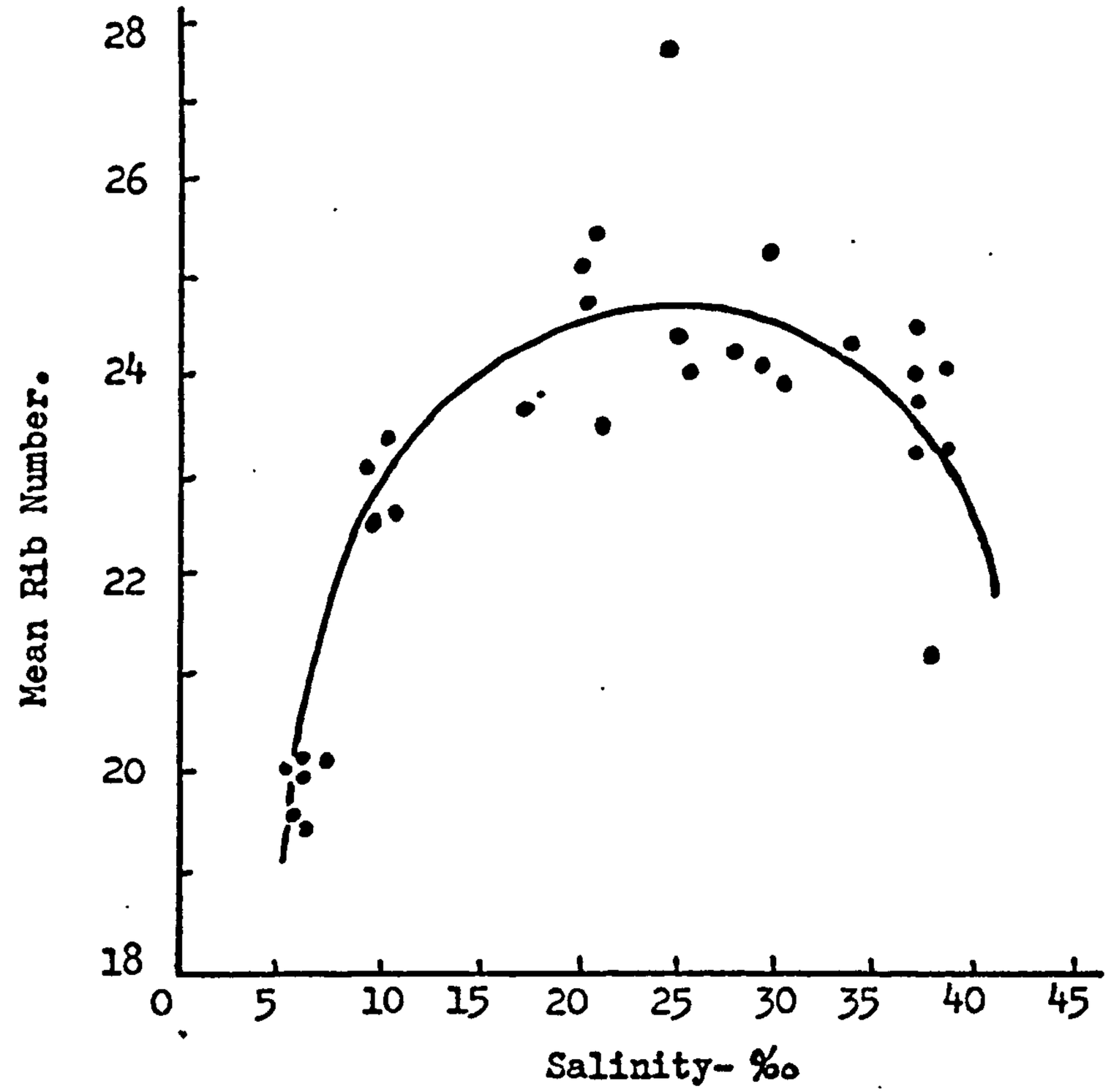


Fig 19 - Relationship of mean rib number to salinity in various lagoon populations of C.glaucum.

Aral Sea, exhibited a decrease in M.R.N. as the salinity of the evaporating lakes he studied increased. Finally, over a salinity range of 5 - 20‰ the average rib-number of C. glaucum increases, which in some part supports the conclusions drawn by Eisma (1965) and shown in fig. 17.

One lagoon locality, Horsey Island Lake, Portsmouth gave a very high mean rib number for the salinity of the environment. This sample was large (100 individuals) and the validity of the M.R.N. has been confirmed independently by Russell (1969). The salinity is likely to be fairly constant as entry of water is afforded only rarely at high tide through sluice gates. An obvious difference between this site and other lagoons, is the fact that it is relatively deep, about 10 metres. It may well be that hydrostatic pressure could be another environmental parameter which affects rib-number within the Cerastoderma.

It can be seen in table 9, considering C. glaucum from the Fleet, Dorset, that those cockles collected from a permanently submerged locality at Langton Heering, in water of 29.2‰, exhibit a higher rib number than the stunted C. glaucum from a littoral location nearer the Fleet entrance, bathed by water of 33.6‰ salinity. It may be that the increase of stress in the form of aerial exposure and/or wave action affect these latter cockles inhibiting rib formation.

Alternatively these C. glaucum fall within the framework of the relationship shown on fig. 19, assuming that the maximum rib number is produced in water of about 30‰. However, Russell (1969) has shown a similar reduction phenomena in the M.R.N. of Danish C. glaucum where the salinity is nearer 15‰.

Thus it would seem that the factors controlling rib-number differ in the two cockles; in response to stagnant environments C. glaucum exhibits one pattern with reference to salinity, whilst C. edule living in tidal localities shows a more directly relatable response to salinity.

(g) Conclusions concerning salinity tolerances of the Cerastoderma.

The discontinuity of Eisma's data reproduced in fig. 17 can therefore be explained by the fact, that the lower portion of the graph represents predominantly C. glaucum (= lamarcki) in low salinity environments, whilst the upper section comprises C. edule from oceanic, generally more saline localities. Certainly this approach has support in the literature. Höpner-Petersen (1958) does not record C. edule in permanent salinities of less than 18-20‰ in Danish waters, and this has also been noted by Huus (1967). Eisma concludes from his data on Netherland cockles that no populations consisting entirely of C. edule occurred below 16.3‰ salinity. Thus although C. edule is found in estuaries where there may be temporary salinity reduction, it does not appear to be as euryhaline as generally maintained. This cockle would seem to be limited to permanent salinities of between 16.3‰ and 36.5‰.

In contrast C. glaucum (as C. lamarcki) is found in Danish waters from 5.5 - 25.3‰, (Höpner-Petersen, 1958), and in Netherland localities from 5.5 - 29.8‰, (Eisma, 1965). Tulkki (1961) considering C. lamarcki in Swedish and Norwegian fjords records a salinity range of 5.0 - 28.0‰ for this cockle, and he was also able to maintain C. lamarcki for several months in aquaria in waters of between 30 - 33‰ salinity. In the British Isles C. glaucum was found in localities with salinities from 8.7 - 34.7‰. However, during the dry summer of 1970, a salinity of 30‰ was recorded at Widewater, Sussex. The C. glaucum population was found to be living in these salinities. Thus the hypothesis of Tebble (1966) and Huus (1968) that C. glaucum may be a brackish water cockle does not seem to be upheld. In the Baltic, Koli (1961) records C. lamarcki in a salinity of 4.5 - 5‰, and this probably presents the minimum tolerance limit of this cockle.

Within the Mediterranean Eisma (1965) records C. glaucum in salinities up to 38.25‰, whilst Russell (1969) has found this cockle in salinities of 52.0 - 72.8‰. In the Caspian Sea cockles are found at a salinity of 50.46‰ (Birstein, 1936). The upper salinity tolerance limit of C. glaucum is probably around 60 - 70‰ as Zenkevich (1947) also records this cockle in hypersaline lagoons cut off from the sea of Azov, in water of 60‰ salinity.

Thus C. glaucum would seem to be extremely euryhaline, tolerating in the Baltic a minimum of about 5‰ and in the sea of Azov a maximum in the region of 60‰. In Britain this cockle would generally appear to be a brackish water cockle, but by extending the study to cover the entire range of this cockle it would seem to be an even more euryhaline animal than C. edule.

The ecological requirement, or necessity, for stagnant saline conditions, or the inability to tolerate exposure to wave action, would seem to be the most important factor(s) controlling the distribution of C. glaucum. The salinity of the environment appears to be far less important. The inability of C. edule to tolerate stagnant environments automatically precludes it from many brackish water localities and from the Baltic sea, where low salinities occur, and from the Mediterranean, where high salinities are found. Thus, in the environments where the Cerastoderma naturally occur C. edule would seem to be less euryhaline than C. glaucum.

4. Shell weight of cockles from the mixed Crouch population.

Invariably C. glaucum collected from lagoon populations are thin-shelled, whereas C. edule from a typically littoral environment are thick-shelled. Thus in the literature (Benthem Jutting, 1943; Boettger, 1950; Remane, 1958) considering Baltic C. lamarcki (= glaucum), recognise that in brackish waters this cockle is thin-shelled. However, in the estuarine environments of the Crouch and Roach, Essex, both cockle types are thick-shelled.

Shell weights of the Cerastoderma from the common environment of the Crouch estuary were compared, to determine if shell deposition, reflected in the shell weights, was similar in the two cockles.

Within the literature, Van Straaten (1957), and Eisma (1965), have used shell length to indicate shell size, but as has already been pointed out in this study, for comparative purposes shell depth (= height) was considered to be the best indication of cockle size. The shells of living cockles were cleaned measured and the tissue removed. The two valves of each individual were then placed in an oven at 100°C for three days and the dry weight obtained. The cube of the shell depth was plotted against dry shell weight - see fig. 20. Clearly there is no difference in the relationship of shell height^3 to shell weight between the two Cerastoderma from a common environment. In a mixed population C. glaucum apparently deposits shell at an equal rate to C. edule and thus thethin nature of shells from many lagoon populations is unlikely to be genetic in origin, but is probably dictated by environmental characteristics such as availability of food, stagnation, ionic balance, calcium content, etc., associated with brackish waters. It could also be concluded, as the shell weights are so similar in the two cockles, that the growth rates are also similar in the two cockles.

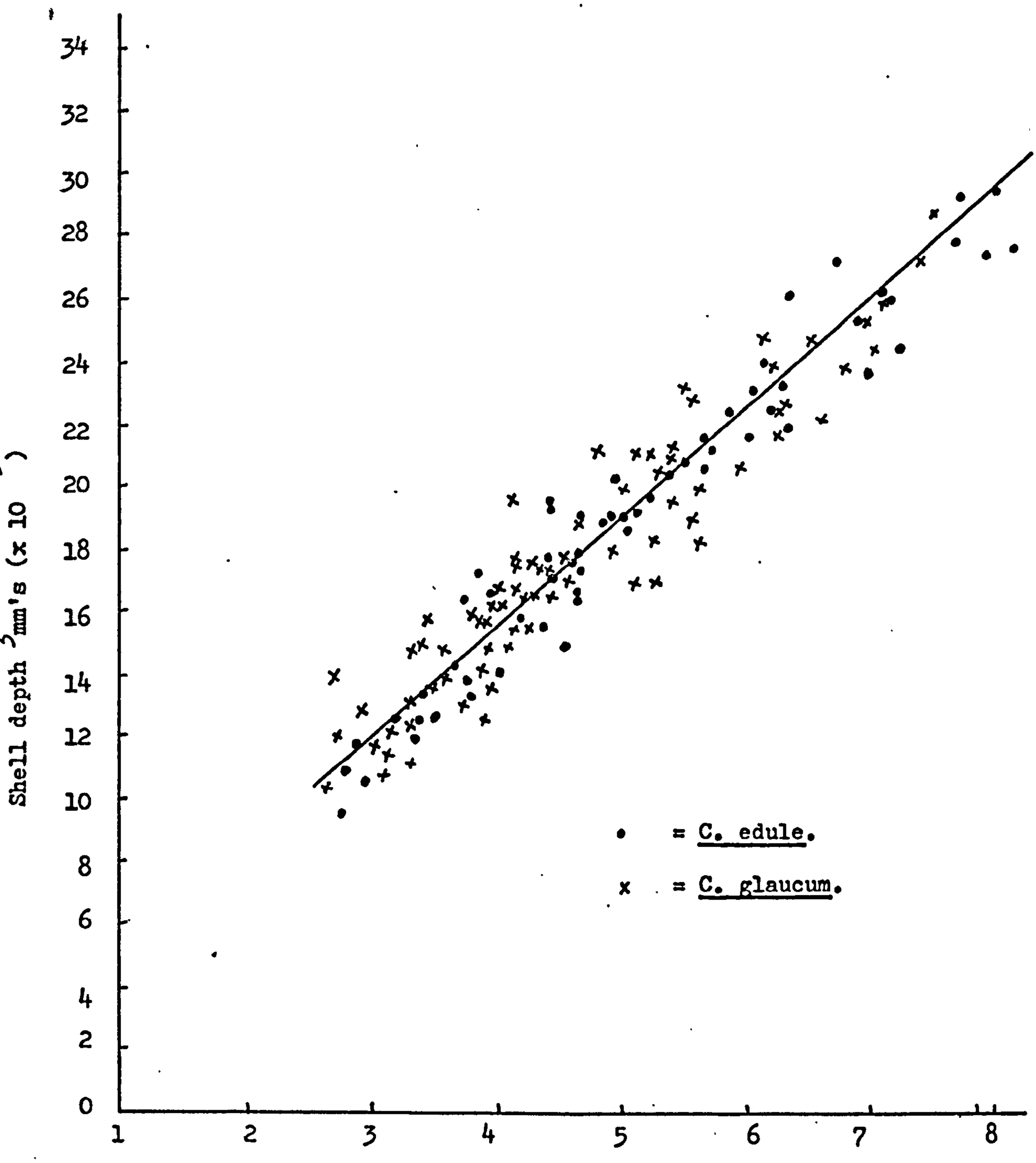


Fig 20 - Relationship of shell depth (mm's)- (cubed) to shell weight (grams) in the two Cerastoderma from the Crouch mixed population.

5. Comparison of tissue weights in the Crouch Cerastoderma.

The tissue weights of C. edule and C. glaucum from the Crouch estuary were determined immediately upon return to the laboratory on the 8.12.68. Shell depths were measured by vernier calipers to the nearest 0.05 mm. The tissues were scraped from the shell, and washed by distilled water, dry weights being obtained by difference, after three days drying in an oven at 80°C.

The relationship of shell depth mm's to dry tissue weight gms. for the Crouch C. edule and C. glaucum is shown in fig. 21. Clearly in the winter, as the relationship is the same in the two cockles, the parameter of shell depth can be used as an indication of size for comparison purposes between C. edule and C. glaucum. The graphs obtained for shell length to dry tissue weight, and shell breadth to dry tissue weight differed in the two cockles. Also in the summer depending upon spawning, C. edule tends to have a slightly greater dry tissue weight compared with C. glaucum.

In addition there did not appear to be any difference in the relationship of dry to wet tissue weight (fig. 22) between the cockles from the Crouch estuary. However, one component of the tissue , the digestive gland, did differ between the two cockles. This difference is shown graphically in fig. 23 where dry weight of digestive gland is plotted against total dry weight of tissue. Clearly the volume of digestive gland in the winter months is considerably greater in C. glaucum compared with C. edule.

It is noted, however, that in the spring and summer the volume difference of digestive gland as estimated by eye, between C. edule and C. glaucum is much less obvious. A seasonal change in volume of digestive gland may well occur in C. edule; but this is much less noticeable in C. glaucum. A change of this nature may not be entirely unexpected as

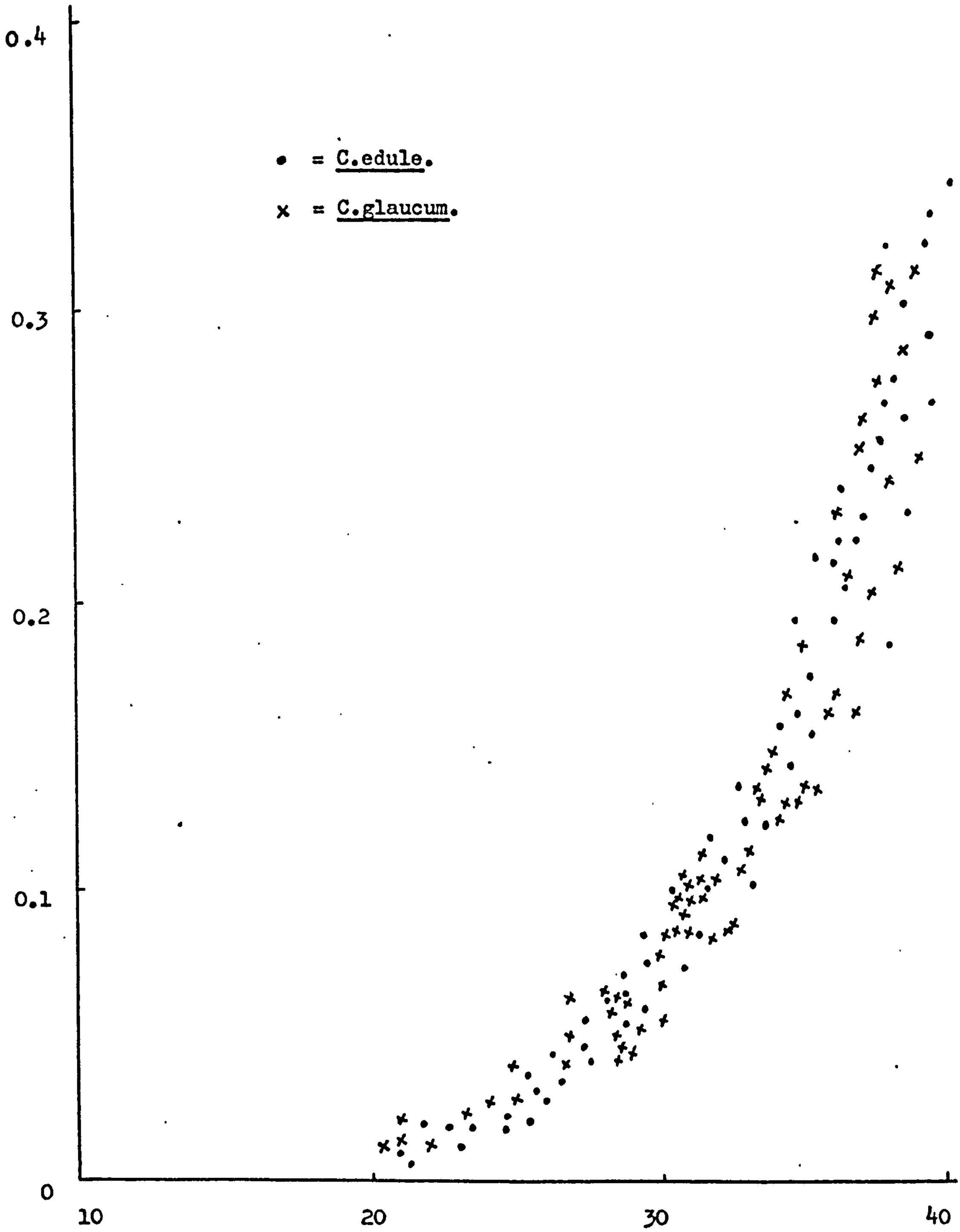


Fig 21 - Relationship, in winter, of shell depth to dry tissue weight in the two Cerastoderma collected from the Crouch mixed population.

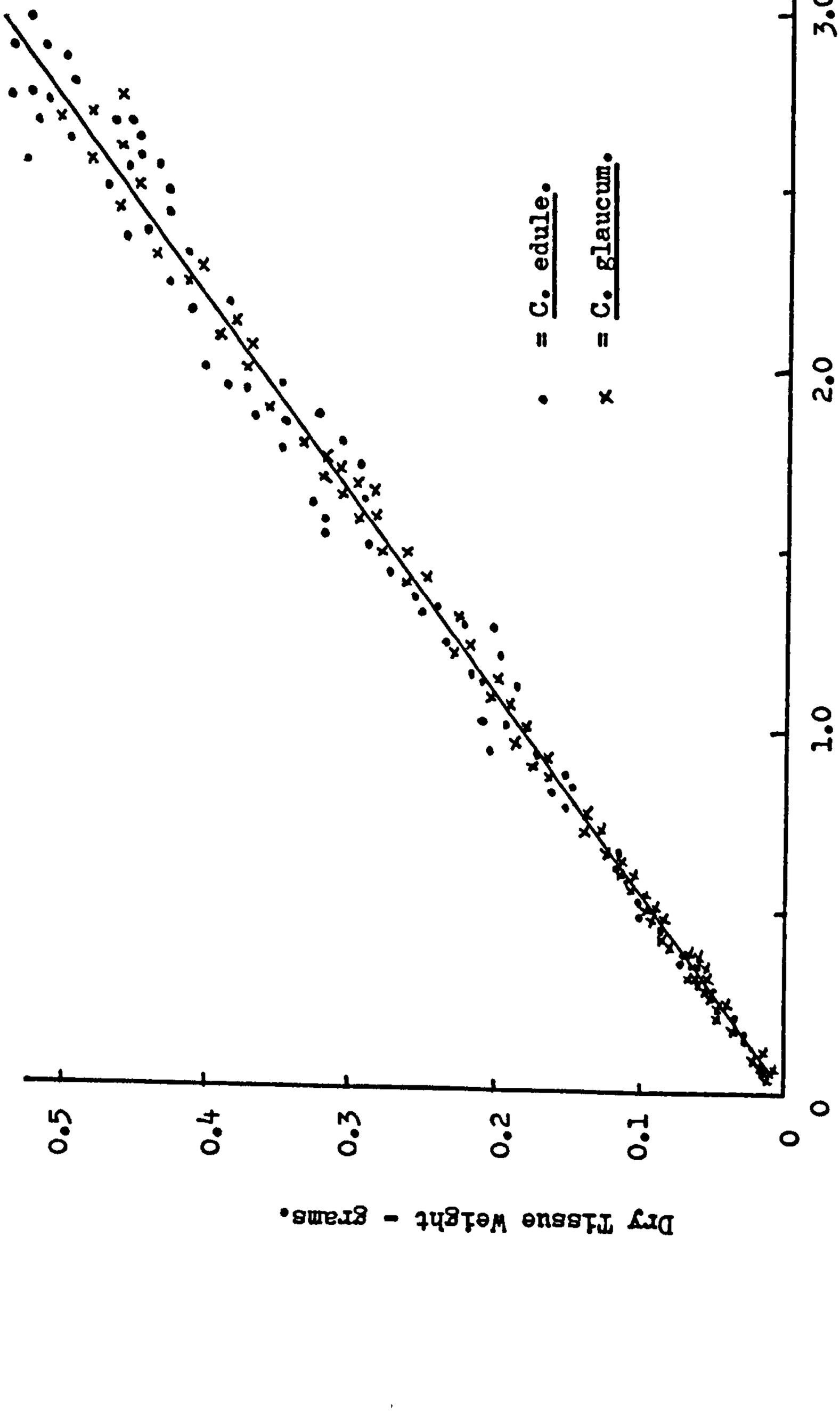


Fig 22 - Relationship of dry to wet tissue weight in the two Cerastoderma from the mixed Crouch population.

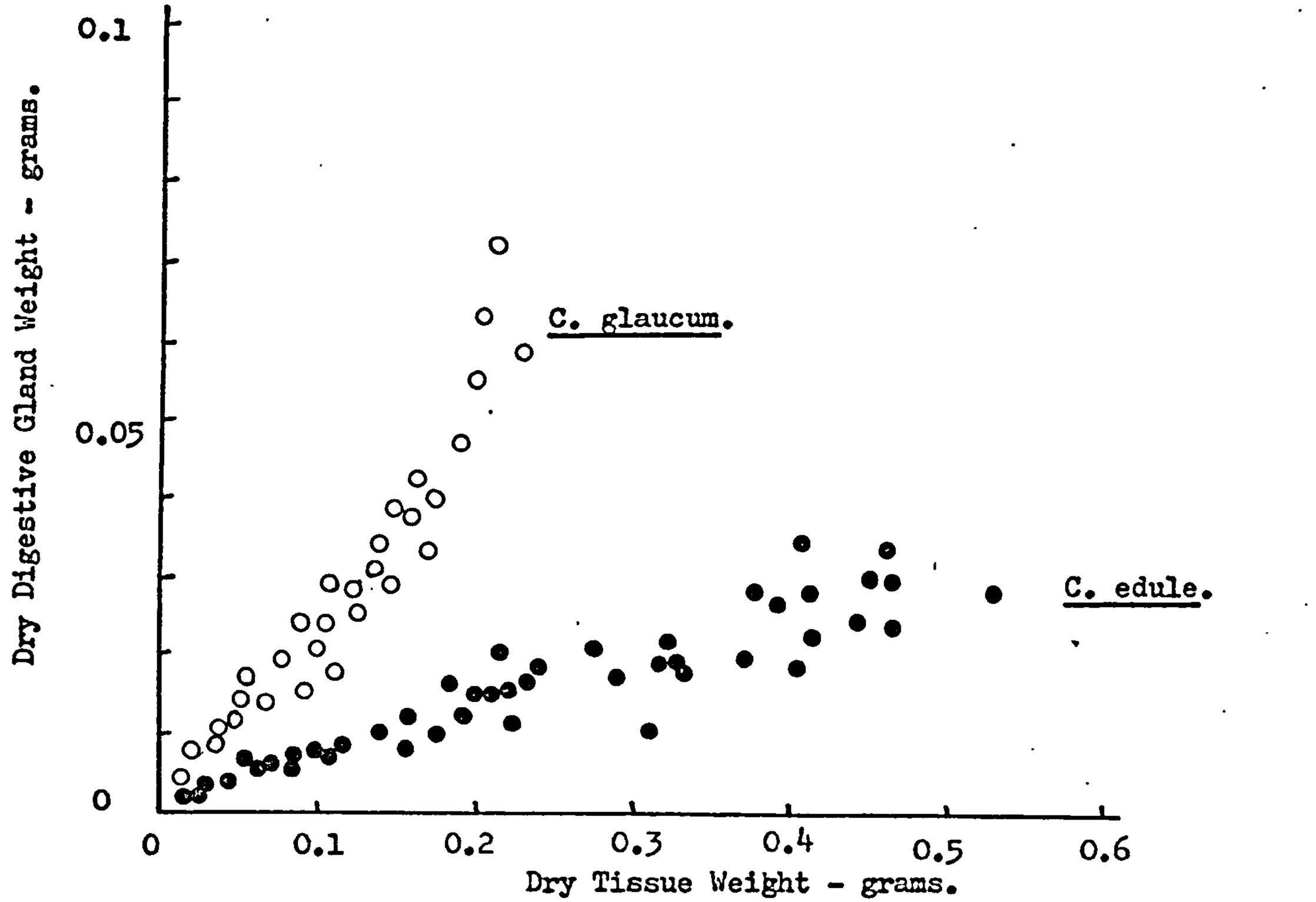


Fig 23 - Relationship of dry digestive gland weight to total dry tissue weight in the two Cerastoderma from the Crouch mixed cockle population.

Morton (1970) has recently shown that C. edule undergoes rhythmic changes in enzyme secretion from the digestive gland, associated with tidal conditions. However in this ~~also in the~~ Scallop Aequipecten irradians, Sastry (1970) has shown that the digestive gland index, indicative of tissue volume, varies throughout the year. However, the lowest index occurred during the summer months and the highest during the winter. In C. edule it may well be that the digestive gland volume is determined more by the quantity and type of food available, than by the reproductive demands of the animal.

REFERENCES - not cited previously

BENTHEM JUTTING, W.S.S. Van., 1943. Lamellibranchia. Fauna van Nederland, Vol. 12, Mollusca (I) C, A.W. Sijthoff, Leiden.

BIRSTEIN, J.A., 1936. The growth and propagation of Cardium edule of Mertvy Kultuk and Kaidak in Caspian Sea in connection with salinity. C.R. (Doklady) Acad. Sci. U.R.S.S., Vol. 4, pp. 195-199.

COLE, H.A., 1956. A preliminary study of growth rate in cockles (Cardium edule L.) in relation to commercial exploitation. J. Cons. perm. int. Explor. Mer. Vol. 22, pp. 77-90.

CRISP, D.J. etal, 1964. Ed. 'The effects of the severe winter of 1962-63 on marine life in Britain'. J. of Anim. Ecol. Vol. 33, pp. 165-210.

DAVIS, D.S., 1967. The Marine Fauna of the Blackwater Estuary and Adjacent waters, Essex. Essex Nat. Vol. 32(1), pp. 2-61.

FRANKLIN, A. & PICKETT, G.D. 1968 Cockle resources of the Wash, 1967-68. Min. of Agri., Fish and Food, Shellfish Information Leaflet, No. 11.

FRASER, C. McL., 1931. Notes on the ecology of the cockle Cardium corbis Martyn. Trans. Roy. Soc. Canada. Vol. 25, pp. 59-72.

GEORGE, T.N., 1924. Variation in the shell of the common cockle. The Naturalist, Vol. 49, pp. 233-239.

GREEN, F.H.W., 1940. (as cited by Cole, 1956 above) Poole Harbour: a hydrographic survey 1938-9. London.

GREEN, J., 1957. The growth of Scrobicularia plana (da Costa) in the Gwendraeth estuary. J. mar. biol. Ass. U.K. Vol. 36, pp. 41-47.

HARRIS, D., 1968. A method of separating two superimposed normal distributions using arithmetric probability paper. J. anim. Ecol. Vol. 37, pp. 315-319.

HOUSE, N.R. and FARROW, C.E., 1968. Daily growth banding in the shell of the cockle Cardium edule. Nature. Vol. 219, pp. 1384-1386.

JAYAKAR, S.D., 1962. A biometrical study of natural selection in Cardium edule. Cah. biol. mar. Vol. 3. Cah. 2, pp. 129-136.

KREGER, D., 1940. On the ecology of Cardium edule L. Arch. Néerl. Zool. Vol. 4, pp. 157-200.

KRISTENSEN, I., 1957. Differences in density and growth in a cockle population in the Dutch Wadden Sea. Arch. Néerl. Zool. Vol. 12, pp. 351-453.

MASON, J.1957.The age and growth of the scallop (Pecten maximus L.) in Manx waters. J. mar. biol. Ass. U.K. Vol. 36, pp. 473-492.

McINTYRE, A.D., 1970. The range of biomass in intertidal sands with special reference to the bivalve Tellina tenuis. J. mar. biol. Ass. U.K. Vol. 50(3), pp. 561-576.

NEWELL, G.E., 1954. The Marine Fauna of Whitstable. Ann. Mag. Nat. Hist. Ser. 12. Vol. 7, pp. 321-350.

ORTON, J.H., 1926. On the rate of growth of Cardium edule. Part I. Experimental observations. J. mar. biol. Ass. U.K. Vol. 14, pp. 239-279.

QUAYLE, D.B. (1951-1952). The rate of growth of Venerupis pullastra (Montagu) at Millport, Scotland. Proc. Roy. Sci. Edin. (B) Vol. 64, pp. 384-406.

REMANE, A., 1958. Oekologie des Brackwassers. In: Die Biologie des Brackwassers. Die Binnengewasser. Vol. 22, pp. 1-216.

SASTRY, A.N., 1970. Reproductive physiological variation in latitudinally separated populations of the Bay Scallop Aequipecten irradians Lamarck. Biol. Bull. Vol. 138, No. 1, pp. 56-65.

SEED, R., 1969. The Ecology of Mytilus edulis L. (Lamellibranchiata) on exposed Rocky Shores, II. Growth and Mortality. Oceologia (Berl.), Vol. 3, pp. 317-350.

SEGERSTRÅLE, S.G., 1960. Investigation on Baltic populations of the bivalve Macoma baltica (L). Commentat. biol. Vol. 23(2), pp. 1-72.

SLIJPER, E.J., 1926-1929. Unfinished manuscript on Cardium edule (L). Rijksmus Nat. Hist., Leiden.

SMIDT, E.L.B., 1944. The effects of Ice Winters on marine littoral faunas. Folia. Geogr. Danica. Vol. 2, pp. 16-21.

SPOONER, G.M. & MOORE, H.B., 1940. The Ecology of the Tamar Estuary VI. An Account of the macrofauna of the intertidal muds. J. mar. biol. Ass. U.K. Vol. 24, pp. 283-330.

STEPHEN, A.C., 1931. Notes on the biology of certain lamellibranchs on the Scottish coast. J. mar. biol. Ass. U.K. Vol. 17, pp. 277-300.

STEPHEN, A.C., 1932. Notes on the biology of some lamellibranchs in the Clyde area. J. mar. biol. Ass. U.K. Vol. 18, pp. 51-68.

STEPHEN, A.C., 1953. Life on some sandy shores in 'Essays in Marine Biology, The Richard Elmhirst Memorial Lectures', pp. 50-72.

STEVENSON, J.A. & DICKIE, C.M., 1954. Annual growth rings and rate of growth of the giant scallop Placopecten magellanicus (Gmelin) in the Digby area of the Bay of Funday. J. Fish. Res. Board Canada. Vol. 11, pp. 660-671.

THAMDRUP, H.M., 1935. Beiträge zur Ökologie der Wattenfauna auf experimenteller Grundlage. Medd. Komm. Danm. Fisk-og.Havunders. Serie. Fisk, Vol. 10, (2), pp. 1-125.

TULKKI, P., 1961. The presence of Cardium lamarcki in Norwegian waters. Sarsia, Vol. 4, pp. 55-56.

VAN STRAATEN, L.M.J.U., 1957. The excavation at Velsen. The Holocene deposits. Verh. Kon. Ned. Geol. Mijnb. Gen., Geol. ser., Vol. 17, pp. 158-183.

WALTON, C.L., 1919. Notes on the shell of Cardium edule. Trans. Liverpool Biol. Soc. Vol. 34, pp. 134-136.

ZENKEVICH, L.A., 1957. Caspian and Aral seas. Geol. Soc. Amer. Memoir 67. Vol. 1, pp. 891-916.

SECTION - VI

SECTION VI

A COMPARATIVE ANALYSIS OF THE REPRODUCTIVE CYCLES OF THE COCKLES CERASTODERMA EDULE (L) AND CERASTODERMA GLAUCUM (POIRET)

Introduction

The criterion of species rank, has in the past been based on easily recognisable morphological characteristics. It was assumed that reproductive isolation and morphological differences proceeded hand in hand, a fact which is increasingly being shown to be untrue. It is the non-interbreeding of natural populations which is the decisive species criterion (Mayr, 1963). Biological mechanisms are properties of organisms which prevent interbreeding in sympatric populations (Mayr, 1957).

The two cockles Cerastoderma edule L. (= Cardium edule L.) and Cerastoderma glaucum (Poiret) (= Cardium lamarcki Reeve) are morphologically very similar. In fact in past literature, C. edule has been regarded as an extremely variable species with several 'ecotypic' varieties (Grossu, 1961; Eisma, 1965); as two separate species (Mars, 1951; Høpper-Petersen, 1958); and finally as consisting of 3 to 5 separate species, (Coen, 1915; Winkworth, 1932 and Chavan, 1945). This last concept has not been further substantiated.

The problem investigated here is whether the cockles C. edule and C. glaucum are varieties of the same genotype or separate species.

C. edule, the common commercial cockle, is found widely distributed around the coast of the British Isles, usually on intertidal sand or mud

flats and in estuaries. The ecology of C. glaucum is less well known. It has been discovered that this cockle is found typically in saline lagoons, isolated from tidal influences (Boyden, 1969), ~~however,~~ although very occasionally C. glaucum does occur intertidally. In stagnant pools this cockle is often the major lamellibranch element of the bottom fauna. The majority of these lagoons in the British Isles occur around the south-east coast of England from North-Norfolk to Dorset, (Boyden, 1969; Russell, 1969); although they can also be found quite commonly on the western Irish coats, (see Section IV). Populations of C. edule have never been found in such stagnant saline localities.

Typically, therefore, reproductive isolation is effected by habitat differences which are reflected in the ecological preferences of the two cockles. Mayr (1949) considers that divergent, allopatric speciation, requires the establishment of sufficient differences so that reproductive isolation is effective even if later the original populations come together again. The object of this reproductive study was to determine the presence or absence of such reproductive isolation in a mixed population of the two cockles, where the two cockles coincide under circumstances which appear to fit Mayr's concept.

An extensive mixed population occurs in the estuary of the River Crouch, Essex; (for further details see Section IV). This sympatric population has enabled the study of the reproductive biology of both cockles, in a situation where differences could not be attributed to differences in the environment. The reproduction of these cockles has been investigated, to determine whether there is isolation between the two cockle types.

Cross Fertilisation Experiments

The object of these experiments was to determine if cross fertilisation between C. edule and C. glaucum was possible. The majority of cockles used in this study originated from the naturally occurring Crouch mixed cockle population, where cross fertilisation might occur. The criterion of successful fertilisation was the production of either rotating trochophores within the gelatinous outer egg envelope, or free veligers. No attempt was made to rear the larvae.

It was found that gametes obtained from spawning individuals were more viable than those obtained by gonad rupture from apparently ripe individuals. Unfortunately, in the time available for this work, spawning could not be induced in the laboratory either by temperature increase or by the addition of suspensions of gametes to the water.

Spawning was, however, observed in a male C. edule transfered from 15°C to 8°C, but other individuals could not be induced to spawn by similar treatment, so it is not clear whether mechanical disturbance, change of water or temperature drop had caused the sperm release. Russell (1969) observed several spawnings in the laboratory of both C. edule and C. glaucum, and he regards the changing of sea water in which the animals are maintained as being important. He also noted spawning in some C. glaucum collected from the French Mediterranean coast and suggested that this was due to a decrease in both temperature and salinity. Because of the lack of a successful method to induce spawning, artificial fertilisation techniques were employed.

The larval stages of C. edule have been described by Lebour (1938), Barker-Jørgensen (1946) and Creek (1961). All these workers reared

artificially fertilized ova in plunger jars. Lebour was able to rear larvae throughout the summer from April to October, but Creek records that fertilisations were most successful at or near the time of spawning in the natural populations.

In the artificial fertilisations conducted here, very ripe individuals (those pertaining to Grade IV of the gonad analysis section) were used, but occasionally only Grade III C. edule could be obtained during the summer months, after the initial spring spawning of this cockle (see later).

Materials and Methods

Adults of both cockles were collected from the Crouch mixed population during the spawning seasons of 1968 and 1969. Other individuals were also gathered at Southend, (= C. edule); and from lagoons at Widewater and Cuckmere Haven, Sussex (= C. glaucum). They were brought back to the laboratory and placed in filtered sea water. Individuals were isolated from each other for at least 6 hours before use in experiments.

Sea water (either water from Burnham laboratory, salinity C.32-34‰ or from the Bay of Biscay, salinity C.33-34‰), was filtered through glass wool, pasteurised by heating to 60°C. three times, (following cooling to room temperature), and finally filtered through an oxoid membrane of 500A° pore size under suction. The water was then re-aerated. All apparatus was sterilised either in an autoclave or oven prior to the experiments.

Individuals were opened and the visceral wall covering the gonad ruptured if this was found to be necessary. The ova were separated from

Table 1 - Results of fertilisation experiments conducted during the 1968 spawning season.

Date of experiment	Period of spawning of cockles (determined by gonad study).	Origin of sea water used in experiment.	Cockle type and sex of individuals of cross.							
			Homozygous		Hybrid		Homozygous		Hybrid	
			F	M	F	M	F	M	F	M
			C.edule		ed x gla		C.glaucum		gla x ed	
6. 5.68	ed	Burnham	P		-		-		-	
14. 5.68		"	P		Ab.		Ab.		Ab.	
		Lagoon cockle cross (Widewater x Cuckmere) P								
21. 5.68		"	P		Ab.		Ab.		Ab.	
		Lagoon cockle cross (Widewater x Widewater) P								
5. 6.68		Biscay	Ab.		Ab.		P		P	
20. 6.68	gla	Burnham	P		P		P		Ab.	
16. 7.68		Biscay	Ab.		Ab.		-		Ab.	

Sex of parent cockle:

F = female

M = male

Concerning cross:

P = larvae present, cross successful

Ab.= cross unsuccessful

- = cross not conducted

Table 2 - Results of fertilisation experiments conducted during the 1969 spawning season.

Date of experiment	Period of spawning of cockles (determined by gonad study).	Origin of sea water used in experiment.	Cockle type and sex of individuals of cross.							
			Homozygous		Hybrid		Homozygous		Hybrid	
			F	M	F	M	F	M	F	M
			C.edule		ed x gla		C.glaucum		gla x ed	
7. 5.69	ed	Biscay	-		-		P		-	
9. 5.69	↓	"	P		Ab.		Ab.		Ab.	
13. 5.69	↓	"	Ab.		Ab.		Ab.		Ab.	
19. 5.69	↓	"	P		P		Ab.		Ab.	
5. 6.69	↓ gla	"	P		P		Ab.		Ab.	
9. 6.69	↓	"	-		-		P		P	

Sex of parent cockle:

F = female

M = male

Concerning cross:

P = larvae present, cross successful

Ab.= cross unsuccessful

- = cross not conducted

other gonadial material by teasing the gonad apart using forceps, and gently shaking the tissue in small beakers containing 15 mls. of filtered water. Tissue fragments were removed and the ova (between 7,000 to 20,000) introduced into 500 ml. of water contained in experimental bowls. A few drops of sperm suspension, obtained in a similar manner to the ova was introduced by pipette, and the bowl covered to prevent evaporation. Each bowl was aerated gently with washed compressed air to maintain water movement. The air was filtered through a dust trap to reduce infection by air borne bacteria. The bowls were examined at intervals to determine the presence of rotating trochophores and free veligers.

All experiments were conducted at 15°C. in a constant temperature room in an approximately 12 hour light/dark regime. It was discovered by an initial experiment that higher temperatures, although promoting rapid larval development also encouraged very rapid bacterial growth. Thus rotating trochophores could be produced in 22 hours at 25°C., about 36 hours at 20°C, and 48 hours at 17.5°C. and 15°C. 15°C. was selected for convenience and in an attempt to prevent excessive bacterial infection.

Results

The major feature of tables 1 and 2 is the high number of failures in fertilisation. This probably reflects a wide variation in actual maturity of individuals that appeared to be ripe. Thus initial fertilisations conducted on 6.5.68 showed that individuals of C. edule from the Crouch population could easily be crossed, whereas an experiment conducted at the same time using Southend C. edule failed to produce veligers. The hybrid using female Crouch C. edule was successful, but

the fertilisation using female Southend C. edule was a failure. This would appear to indicate that the condition of the gametes from the female parent is particularly important in obtaining successful fertilisations, a conclusion also reached by Creek (1961). It is very likely that the addition of gonad and tissue fluid extract, unavoidable in artificial fertilisations, affects both fertilisation of ova and development and survival of larvae, as has been shown for Echinus by Wilson and Armstong (1954). Loosanoff (1937) drew attention to the fact that in Mercenaria mercenaria although the gonads frequently appeared to be ripe when examined histologically, this was not an indication that they were physiologically mature. In this species the usual methods of artificial fertilisation always give negative results, a fact that it also true of Venus striatula, (Ansell, 1961) and Cyprina islandica, (Loosanoff, 1953).

It can be seen from tables 1 and 2 that successful homozygous fertilisations using parent C. edule were made in May and early June, whereas successful homozygous crossing of C. glaucum occurred later in the season. Hybridisations between C. edule and C. glaucum were successful in the laboratory. Rotating trochophores and veligers were obtained in both crosses using either cockle as the female. Kingston (Personal communication) has reared to settlement, hybrids between the two cockles and thus it would seem that it is not differences between the gametes of the two cockles that prevents the development of crosses. Whether these intermediates are reproductively viable is of interest. Certainly one intermediate adult, possessing shell morpholcgical characteristics of both cockles (but containing a black, globular digestive gland indicative of C. glaucum), produced veligers when crossed with C. glaucum. Thus, there is no reason to suppose that intermediates should not be capable of producing progeny.

The maintenance of the two almost completely distinct cockle populations, in a sympatric association in the Crouch estuary is therefore probably not the result of the inability of gametes to produce hybrids, but rather that some other isolation mechanism is responsible.

Previous studies on the reproductive cycles of the Cerastoderma

Previous work has been mainly confined to the commercial cockle Cerastoderma edule. Johnson (1899) describes fully the anatomy of the ripe gonad prior to spawning and this has been extended by Creek (1967) to include the remainder of the year.

The period of maximum spawning occurs in the spring. Johnson records spawning at the end of February or the beginning of March, Orton (1926) from March to April and Cole (1956) from April to June. Orton (1933), investigating the Morecambe Bay cockle fishery, states that spawning begins in April.

Creek (1967) studying a cockle population of C. edule in the Dovey estuary, recorded spawning in 1953 during the last week of May, whilst in the cool spring of the following year, 1954, this was delayed until the first week of June. She also found that gonads were mature from February until late May. Handcock (Personal communication) has studied the gonad condition of C. edule from various commercial populations around Britain. He used a classification of gonad maturity similar to that described in this study. Developing gametes were discovered in cockles from The Wash and Llandrydan (South Wales) from January, and spawning occurred before mid-June in cockles collected from this latter locality during 1960. Large quantities of gametes were found in the gonads as late as the 30th June in individuals gathered from the Polard spit, North Kent.

It may well be that the rapid gametogenesis that occurs in the Cerastoderma, coupled with the equally rapid voiding of gametes at spawning, deceived earlier workers as to the actual timing of this process. Nevertheless, there appears to be some variability in the timing of the initial late spring spawning between different populations of C. edule.

Individuals containing gametes have been found throughout the summer (Orton, 1920; Wright, 1926; Thorson, 1946), thus it appears possible that C. edule sheds gametes at intervals throughout this period. Certainly Lebour (1938) was able to obtain fertilised ova of C. edule between April and September, but most readily between May and August. Veligers have been recorded in the plankton from June until October, (Orton, 1933).

The planktotrophic larval life of C. edule appears to be in the region of 5 weeks (Lebour, 1938), but Creek (1961) is of the opinion that larval life may be as short as 2 to 3 weeks. Certainly as Orton (1933) collected spat in quantity towards the end of June, and in view of the suggested duration of planktonic life, it would appear that the middle of May, not April would have been a more accurate estimate of spawning on the Morecambe beds during the period of Orton's study.

The only recorded work on the breeding cycle of C. glaucum is that of Hopper-Petersen (1958). He studied only a few individuals from two Danish fjords, recording that in April the cockles had hardly begun to mature', and that 'sexually mature' cockles occurred from mid-May onwards.

Material and Methods

Samples of C. edule and C. Glaucum were collected between May 1968 and September 1969, from the Crouch mixed population near Hullbridge 'ferry' Essex. Cockles were gathered by hand from between Extreme Low Water Springs (E.L.W.S.) and Low Water Neaps (L.W.N.). Samples, varying from about 30 - 200 individuals of each cockle type, were made at weekly or bi-weekly intervals during the spring and summer, and at monthly intervals during the winter. Several other small samples were collected from higher tidal levels to determine the effect of shore level upon maturity.

Cockles were examined immediately upon return to the laboratory, or at most within 24 hours of collection. On such occasions they were maintained at 10°C in air. Only cockles with over two winter rings, usually those with between 3 - 5 annual rings were used for this analysis. The two forms were separated using the shell characteristics of each type described earlier. - (See Section II).

Estimation of the reproductive condition was determined on examination of the following:

1. Macroscopic appearance of the gonads (see later for grading and maturity).

and 2. Microscopic examination of smears of the sexual products.

The shell valves were parted and an estimation of gonad volume made. The visceral mass was then teased apart and smears of the visceral wall with attached gonad was examined at x 100 magnification. All cockles in the survey were sexed and graded on the basis of gonad quantity, and presence or absence of mature or immature germ cells.

Anatomy of Gonads

The reproductive organs of C. glaucum are very similar to those of C. edule as described by Johnson (1899). The gonad consists of paired, branching, tubular glands, opening to the exterior by two pores on either side of the posterior dorsal region of the foot. Gametogenesis occurs in terminal blind endings, the alveoli, from which ducts run to collecting ducts, which are finally channeled into two terminal ducts. The organs are found principally in the peripheral region of the anterior visceral mass. The gonad spreads between the transverse muscles and convolutions of the gut, and interdigitates with the secretory lobes of the digestive gland.

When the gonad is fully developed the visceral mass above the foot becomes distended with gametes. Immediately after spawning the visceral wall becomes flaccid and watery in appearance, and through this the main tubules of the gonad, especially the testes, can be clearly seen.

When ripe, the sexes of C. edule can often be separated by colour, the male gonad is usually paler than the female. This separation is easier in C. glaucum where the massed ova appear orange, and the sperm as cream or white. However, during the summer, because of the loss of gamates this separation on the basis of colour becomes less useful.

Categories of Gonad Condition of the Cerastoderma

Four stages of gonad maturity were recognised in females, whereas only three grades were detectable in males. It was found difficult to separate undeveloped follicles containing spermatocytes and inactive sperm, from interfollicular connective tissue of undifferentiated individuals. This feature has been recognised in other marine

invertebrates, e.g. Spirorbis borealis (Williams, 1965). The general scheme of classification of gonad condition follows that previously used for other molluscs, e.g. Mytilus edulis, (Chipperfield, 1953) and Patella vulgata, (Orton et al, 1956).

The arbitrary grades have been assigned Roman numerals adhering to the scheme of classification adopted by other workers.

Female categories

Grade IV (Very ripe stage)

Gonad volume extensive, visceral mass and lateral wall of upper region of foot distended. Female gonad appears pale orange (especially in C. glaucum). Oocytes large, compacted together in ducts and follicles. Lumina of follicles completely occluded. When shed, oocytes assume a spherical form (egg diameter about 50μ). Fertilisation experiments using gametes from this grade were most successful.

Grade III (Ripe)

Cocytes numerous; as well as many being fully rounded and free within the follicle lumina, some also pyriform in shape. These are often attached to the basement membrane of the follicle wall by a thin stalk (the micropyle). Follicles well developed and prominant.

Grade II

Ovary only about half full of oocytes, and interfollicular connective tissue is plentiful. Before the beginning of May this grade contains numerous, small unripe oocytes, which are budding off from the germinal epithelium. The majority remain attached to the epithelium by a micropyle. Lumen of alveoli not occluded. After partial spawning this grade is represented by those individuals

possessing a few residual ova in the follicles. Small young oocytes develop among these ova and bud off from the germinal epithelium in preparation for later spawning.

Grade I

Traces of ovary only visible upon microscopic examination. During the winter and spring the ovary contains a few, very small developing oocytes, the majority of which are still attached to the germinal epithelium of the follicles. Rapid gametogenesis is occurring and the follicles have relatively large, unoccluded lumina. In the summer, autumn and early winter, this stage represents the near spent or spawned out condition, and the ovary often contains a few large, often irregularly shaped (but not pyriform) unspawned ova. These lie free in the lumen of some follicles. The visceral mass is flaccid in appearance.

Male categories

Grade IV (Very ripe condition)

Gonad volume large and visceral mass distended. Male gonad white or cream. Follicles closely compacted and lumina occluded by free spermatozoa, arranged as in other lamellibranchs, with the heads together, forming dense bands within the follicles. Little tissue visible between the follicles. Spermatozoa active upon microscopic analysis.

Grade III

Morphologically the testis is very similar to Grade IV, but the quantity of gonad is less, although it still occupies a major portion of the visceral mass. Follicles numerous, spermatozoa active.

Grade II

In the early months of the year this grade accounts for those individuals undergoing rapid gametogenesis. Within the follicles are numerous sperm mother cells and bands of spermatids surrounding the inner follicle wall. There are only a few free sperms, which appear to be inactive. In the summer months, this grade includes those individuals which have undergone partial spawning. In this partially spawned condition the viscera becomes watery and flaccid in appearance and through which the tubular testes can be seen. Large clumps of white/ cream follicles, containing residual active sperm, often remain attached to the visceral wall, especially in C. edule.

In Summary:

Grades III and IV

Individuals of grade IV maturity extrude gametes into the mantle cavity when the shell valves are parted, whilst in those of Grade III the gonad is not ruptured upon valve separation, but gametes are freely released when the visceral wall is cut.

The most mature grades are, therefore, represented by Grades III and IV. These individuals are about to spawn, or are in the process of spawning, or have just spawned at the time of collection. The appearance of the ova was a good guide to separate the two ripest grades. Individuals with abundant rounded ova were separated from those with loosely packed ova, indicating partial spawning, and those in a developmental stage containing some pyriform eggs.

Grades I and II

These grades either represent the immature developing stages or later in the season the re-developing or the almost spent condition,

depending upon the date of examination. After the initial spawning peak of mature individuals, re-development of the oocytes especially in C. edule does occur during the summer months. The visceral mass is flaccid in appearance in spawned individuals.

Grade C(N)

After spawning there is a resting spent condition when individuals possess no gametes. These fall into the grades of undifferentiated, indeterminate, or neuter of other workers. The 'gonad' is represented by a small quantity of bright orange germinal tissue attached to the visceral wall. This stage appears to be maintained over the winter in a large percentage of individuals. The flesh of grade C individuals in summer and autumn is extremely flaccid and watery in appearance.

The grades of gonad maturity used in this study are shown on table 3.

The visceral mass of the Cerastoderma is often infected by larval digenetic trematodes, which, if the infection is extensive, results in complete castration of the gonad. A full account of incidence of infection by these trematodes is found elsewhere (see Section VII). These parasitised neuter individuals have been omitted from this study, though their numbers are recorded on table 4.

Results

The cockles, Cerastoderma edule and Cerastoderma glaucum, are both dioecious, and their reproductive cycles essentially follow a similar pattern.

The ratio of males to females is not quite unity (see table 5). The greater number of recorded females reflects the difficulty

Table 3 - Scheme of Classification of Gonad Development in the Reproductive cycles of the Cerastoderma.

Grade 0 (N) - Spent or resting condition. No gametes, no follicles visible. Indeterminate, neuter or undifferentiated.

Male	Female	
Grade -	I	- Beginning to develop, very young oocytes detectable, with or without a few large, residual ova remaining from previous spawning. Onset of gametogenesis.
II	II	- Gametes of both sexes detectable, oocytes larger, follicles active, spermatocytes non - motile.
III	III	- Ripe, large ova, pyriform and round. Active sperm. Gametes released upon rupture of visceral wall.
IV	IV	- Very ripe, gonad distended and fully mature. Follicle lumina completely occluded by gametes. Ova round and free. Gametes released into mantle cavity on opening of shell valves.

Table 4 - Incidence of infection of the two Cerastoderma from the Crouch mixed population by larval Digenea.

Cockle Type.	Total number of each cockle examined.	Nos. infected (invariably castrated) by larval Digenea.	Percentage incidence of infection.
Cerastoderma edule	2,696	354	13.1
Cerastoderma glaucum	2,401	10	0.41

Table 5 - Distribution of males, females, and indeterminate individuals in the two Cerastoderma collected from the Crouch mixed population during the survey from April 1968 to September 1969.

Cockle Type	Total Nos. exam'd	Nos. of males	%age of total	Nos. of females	%age of total	Ratio of males/female
Cerastoderma edule	2,202	777	35.3	940	42.7	1:1.21
Cerastoderma glaucum	2,368	647	27.3	907	38.3	1:1.42

Cockle Type	Nos. of indeterminate individuals.	% age of total.
Cerastoderma edule	485	22.0
Cerastoderma glaucum	814	34.4

experienced in determining initiation of gametogenesis and the almost completely spawned out condition in males. It is assumed that in the Cerastoderma there are equal numbers of males and females. There is no evidence of sex reversal which is found in certain other lamellibranchs (Coe, 1934, 1936). The overall number of indeterminate individuals was greater in C. glaucum than in C. edule, 34.1% to 21.9% in the two respective populations.

Reproductive cycles of the Cerastoderma

Primary spawning in the Cerastoderma of the mixed population took place between May and July. C. edule has a more extended breeding season than C. glaucum, shedding batches of gametes at intervals throughout the summer months, but this spawning involved a much smaller proportion of the population. Some individuals retained or developed sex products during the winter months but the majority of the population remained undifferentiated. The main period of gametogenesis occurred in early spring.

Affect of tidal level upon gonad maturity of the Cerastoderma

The cockle population on the River Crouch extends from the middle estuary, where they are permanently submerged, upshore towards mid-tide level (M.L.T.). Aerial exposure time, thus varies from 0 - 3/4 hours/tide (25 - 33.3% exposure to air). All the cockles were collected from a steep sloping southward facing shore. The gonad maturity of cockle samples collected from different shore levels are compared on table 6. Unfortunately, only low sample numbers could be collected from the higher shore levels, but there are clearly fewer individuals in the most mature categories, Grades III and IV, compared with samples collected

TABLE 6

The Effect of Shore Level Upon the Gonad Maturity of *Cerastoderma*

Collected from the Crouch Mixed Population

Cockle type, date of collection and approx. shore level of sample	No. in Sample	Maturity of Females				Maturity of Males				Indeterminate		Summed Male and Female Results	
		Grade III-IV		Grades I-II		Grades III-IV		Grade II					
		Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	% at Grades III-IV	% at Grades I -II
C.edule													
23.5.68 E.L.W.S.	45	7	16	11	24	13	29	5	11	9	20	45	35
Near M.T.L.	41	-	-	23	56	5	12	9	22	4	10	12	78
C.edule													
13.6.68 E.L.W.S.	85	4	5	36	42	24	29	14	16	7	8	34	58
20.6.68 L.W.N.	22	-	-	11	50	-	-	8	36	3	14	-	86
26.6.68 E.L.W.S.	77	2	3	26	33	22	29	15	19	12	16	32	52
C.glaucum													
13.6.68 E.L.W.S.	92	39	42	6	6	32	35	8	9	7	8	77	15
20.6.68 L.W.N.	16	-	-	4	25	3	19	4	25	5	31	19	50
26.6.68 E.L.W.S.	127	52	41	11	9	40	31	9	7	15	12	72	16

from E.L.W.S. This difference is regarded as real and may reflect the influence of temperature upon gonad maturity in the Cerastoderma.

The temperature of surface muds can be higher than the ambient air temperature on temperate muddy shores, (Battle, 1933); (Kristensen, 1956); (Caddy, 1967). Thus temperature is one of the most obvious environmental parameters which differs in the habitats occupied by cockles between E.L.W.S. and higher levels. Certainly, the cockles from E.L.W.S. are also exposed for only about 30 tides/100 and thus do experience a much more equable temperature regime. Battle (1933) found that the greatest percentage of spent individuals of Macoma balthica occurred in specimens collected from the highest shore levels, with the longest exposure to air. On the other hand Seed(1969), studying Mytilus edulis, showed that there was no difference in maturity between high and low shore mussels from the Yorkshire coast. The reproductive cycles of Macoma, Mytilus and the Cerastoderma differ considerably, thus coordination of spawning may well be affected differently in each type. It could be suggested that Mytilus, living on or above the substrate may experience higher temperatures than Macoma or the Cerastoderma buried within the substratum. The apparent stability of gonad maturity in Mytilus may well reflect an adaptation of this shore animal, in the sense that it may be independent of high or variable temperatures.

In view of the above findings, the animals used in the gonad analysis were collected from a short section of shore at one tidal level (E.L.W.S.) where both cockles were common.

Analysis of spawning with reference to combined maturity of males and females (See tables 7 and 8)

From figure 1 it can be seen that the reproductive cycles of the two Cerastoderma studied are very similar. For details concerning the

Table 7 Combined gonad maturity data showing the distribution of mature & non-mature individuals of both sexes of Cerastoderma edule, calculated as percentage of sample total.

Date of collection	FEMALES: GRADES III-IV Nos.	%	GRADES I - II Nos.	%	Indeterminate Nos.	%	MALES: GRADES III-IV Nos.	%	GRADE II Nos.	%	Numbers castrated by larval Digenea	Sample no. minus parasitised individuals	SUMMARY - Combined males and females: % at grades III - IV	% at grades I - II	% indeterminate
5. 5.68	6	16	16	43	2	5	7	20	6	16	not recorded	37	36	59	5
10. 5.68	16	53	6	20	-	-	6	20	2	7	not recorded	30	73	27	-
15. 5.68	11	32	3	9	-	-	19	56	1	3	2	34	88	12	-
22. 5.68	17	19	23	26	11	12	27	31	11	12	11	89	50	38	12
30. 5.68	-	-	26	30	27	31	19	22	15	17	12	87	22	47	31
6. 6.68	9	7	43	33	33	25	18	15	28	21	8	131	25	54	25
13. 6.68	4	5	36	41	7	8	25	32	13	15	16	85	37	55	8
26. 6.68	2	3	26	33	12	16	22	29	15	19	9	77	32	52	16
11. 7.68	4	4	15	15	7	7	34	34	40	40	12	100	38	55	7
25. 7.68	3	6	18	34	3	5	9	17	20	38	9	53	23	72	15
8. 8.68	-	-	29	46	7	11	6	10	21	33	18	63	10	79	11
22. 8.68	-	-	32	36	18	20	15	17	24	27	19	89	17	63	20
11. 9.68	-	-	23	43	13	25	1	2	16	30	11	53	2	73	25
26. 9.68	-	-	20	40	6	12	8	16	16	32	10	50	16	72	12
24.10.68	-	-	42	34	42	34	2	1	38	31	28	124	1	65	34
21.11.68	14	7	92	46	58	29	4	2	30	16	20	198	9	62	29
21.12.68	-	-	68	43	72	45	-	-	18	12	26	158	-	55	45
22. 1.69	-	-	41	43	46	48	-	-	9	9	19	96	-	52	48
8. 3.69	-	-	39	57	19	28	1	2	9	13	16	68	2	70	28
7. 4.69	-	-	49	50	34	35	-	-	16	15	10	99	-	65	35
22. 4.69	3	4	36	49	22	30	1	2	11	15	8	74	6	64	30
4. 5.69	8	15	14	26	3	6	20	38	8	15	6	53	53	41	6
10. 5.69	8	20	3	8	3	8	24	61	1	3	3	39	81	11	8
18. 5.69	8	19	12	29	2	4	17	41	3	7	11	42	60	36	4
29. 5.69	-	-	10	29	4	12	10	30	10	29	8	34	30	58	12
5. 6.69	3	10	9	31	3	10	9	31	5	17	4	29	41	48	11
15. 6.69	2	4	26	57	2	4	9	20	7	15	5	46	24	72	4
30. 6.69	2	5	8	20	17	43	6	15	7	17	2	40	20	37	43
14. 7.69	3	9	10	30	2	6	8	24	10	30	4	33	33	60	7
27. 7.69	1	3	10	32	4	14	11	35	5	16	6	31	38	48	13
19. 8.69	3	9	12	36	3	9	4	12	11	33	4	33	21	69	10
10. 9.69	-	-	16	46	3	8	2	6	14	40	4	35	6	86	8

Table 8 Combined gonad maturity data showing the distribution of mature & non-mature individuals of both sexes of Cerastoderma glaucum, calculated as percentage of sample total.

Date of collection	FEMALES GRADES III-IV Nos.	%	GRADES I - II Nos.	%	Indeterminate Nos.	%	MALES GRADES III-IV Nos.	%	GRADE II Nos.	%	Numbers castrated by larval Digenea	Sample no. minus parasitised individuals	SUMMARY - Combined males and females % at grades III - IV	% at grades I - II	% indeterminate
5. 5.68	4	10	9	23	6	15	4	10	16	42	not recorded	39	20	65	15
10. 5.68	4	18	2	9	1	4	12	54	3	15	not recorded	22	72	24	4
15. 5.68	10	56	1	5	-	-	7	39	-	-	-	18	95	5	-
22. 5.68	26	40	6	9	6	9	21	34	6	9	-	65	73	18	9
30. 5.68	26	24	6	6	31	29	36	33	9	8	1	108	57	14	29
6. 6.68	20	29	8	12	16	23	20	29	5	7	1	69	58	19	23
13. 6.68	39	42	6	6	7	8	33	38	7	8	-	92	78	14	8
26. 6.68	52	41	11	9	15	12	42	31	9	7	2	127	72	16	12
11. 7.68	14	15	22	23	4	4	40	43	16	16	-	96	57	39	4
25. 7.68	-	-	38	58	3	5	4	7	20	31	-	65	6	89	5
8. 8.68	1	1	28	41	12	18	4	6	23	34	1	68	7	75	18
22. 8.68	-	-	20	22	56	61	2	2	14	15	-	92	2	37	61
11. 9.68	1	2	23	37	28	45	1	2	9	14	-	62	4	51	45
26. 9.68	-	-	24	30	36	45	4	5	16	20	-	80	5	50	45
24.10.68	-	-	21	15	98	70	-	-	20	15	-	139	-	30	70
21.11.68	-	-	75	38	108	54	4	2	12	6	-	199	2	44	54
21.12.68	-	-	46	30	104	68	-	-	2	2	-	152	-	32	68
22. 1.69	-	-	19	18	85	81	-	-	1	1	-	105	-	19	81
8. 3.69	-	-	30	40	43	58	-	-	1	2	-	74	-	42	58
7. 4.69	-	-	59	43	80	57	-	-	-	-	2	139	-	43	57
22. 4.69	-	-	10	18	36	67	-	-	8	15	-	54	-	33	67
4. 5.69	18	20	17	19	19	21	33	38	5	4	-	92	57	22	21
10. 5.69	6	21	2	7	3	11	16	57	1	4	-	28	78	11	11
18. 5.69	18	58	2	6	2	6	8	26	1	4	1	31	84	10	6
29. 5.69	15	32	8	17	2	4	20	43	2	4	-	47	75	21	4
5. 6.69	14	40	3	9	4	11	13	37	1	3	-	35	77	12	11
15. 6.69	29	50	8	14	-	-	15	29	6	10	1	58	76	24	-
30. 6.69	20	31	5	8	1	2	31	53	7	11	-	64	79	19	2
14. 7.69	9	18	13	26	-	-	13	26	14	29	-	49	45	55	-
27. 7.69	1	3	15	45	-	-	8	24	9	27	1	33	28	72	-
19. 8.69	9	21	10	23	1	2	14	34	9	21	-	43	54	44	2
10. 9.69	2	5	22	51	7	16	3	7	9	21	-	43	12	72	16

gonad stages in the Cerastoderma during the period of study see tables 7 - 10.

In C. edule the percentage of indeterminate individuals, after a small peak associated with the spring spawning (see fig. 1), increases gradually during the summer and autumn months, reaching a peak of 48% of the total in January. There then occurs a gradual reduction in the percentage of this grade, falling to a very low value in May and June. This grade is much more prominent in C. glaucum, 82% of this cockle examined in January being undifferentiated. By the beginning of April 57% of the C. glaucum and 34% of C. edule were still indeterminate. In the Cerastoderma, especially C. glaucum, this grade is recognised as an overwintering stage.

The number of non-mature Cerastoderma (Grades I and II) drops sharply in May, but then increases during the summer months reaching a maximum in late July or August. Thereafter, the percentage of this category drops slowly throughout the autumn and winter months. The average percentage during these months is c. 60% in C. edule, but only c. 40% in C. glaucum. The peaks of this non-mature grade closely follow the peaks of ripe individuals (see fig. 1).

The individuals which contained gametes during the winter months were either undergoing slow development, or had residual gametes in the gonad, remaining from the previous summers spawning. These may well be destined for resorption during the winter and spring, or as occurs in Venerupis pullastra, (Quayle, 1961) and Venus striatula (Ansell, 1961), the oocytes may persist through the winter and spring without being resorbed. Creek (1967) distinguished young oocytes in C. edule as early in the winter as November. In the Cerastoderma populations examined here gametogenesis, did not occur until February or even early

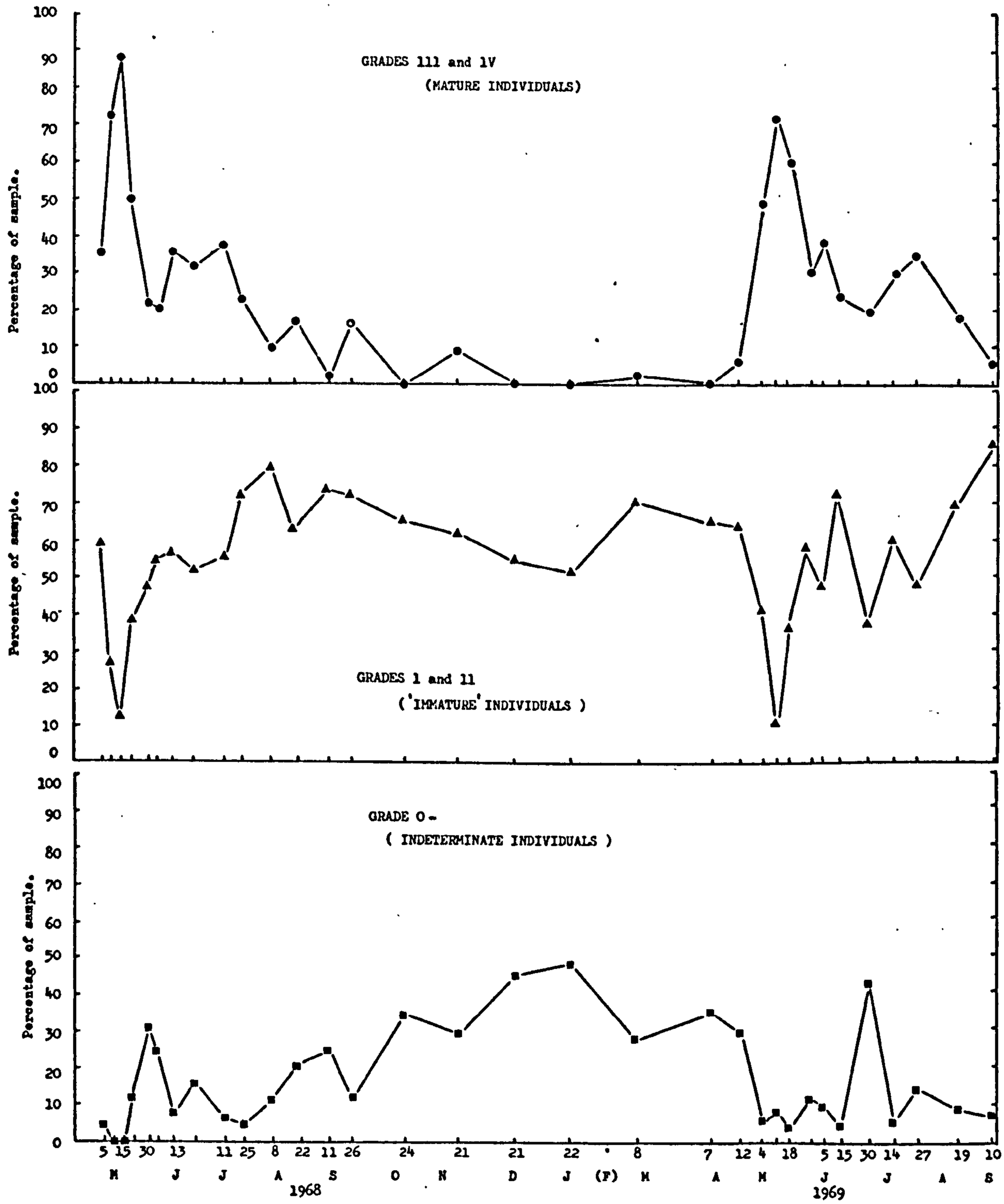


Fig 1 A - Reproductive cycle of C.edule from the Crouch mixed cockle population during the survey from May 1968 until September 1969.
(Data for males and females have been combined - see tables 7 and 8)

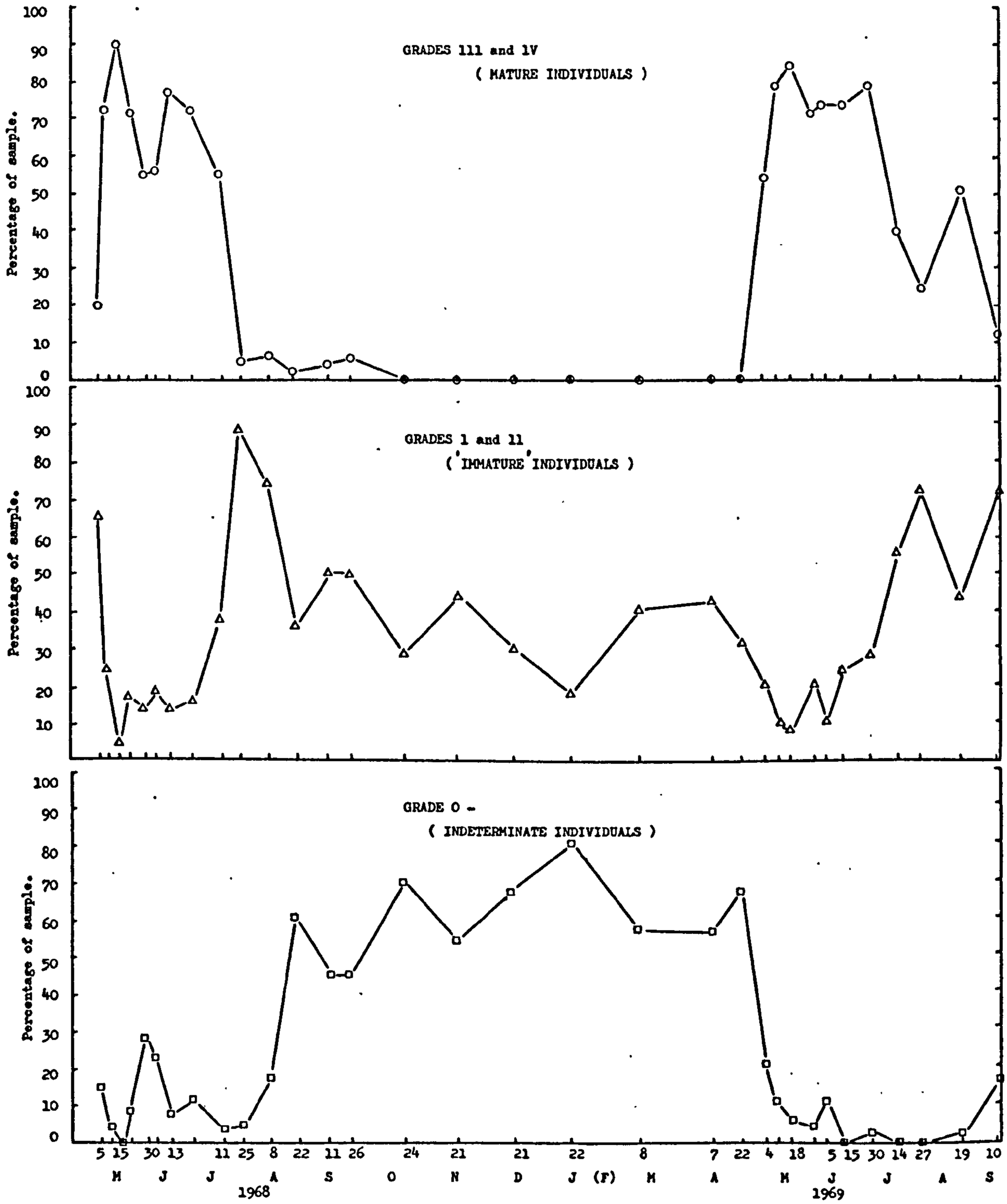


Fig 1B - Reproductive cycle of C.glaucum from the Crouch mixed cockle population during the survey from May 1968 until September 1969.
(data for males and females have been combined - see tables 7 and 8)

March. Very rapid gonad development then occurred during April and the beginning of May, resulting in great distension of the visceral mass.

The rapid gametogenesis in the early spring results in mature individuals (Grades III and IV) by May. The gonads of both cockles attained this stage of development by the 15th May in 1968 and by the 10th May in 1969. In these two seasons C. edule then immediately spawned, whereas C. glaucum retained a high state of maturity. At the height of maturity the percentage of ripe cockles in the two years was, C. edule (78 and 71%) and C. glaucum (90 and 84%). The number of individuals available for spawning is thus greater in C. glaucum than in C. edule. In most lamellibranchs it has been shown that the entire population does not reach ripeness at the same time, (Nelson, 1928; Loosanoff, 1937, 1942, 1953). The Cerastoderma, especially C. edule, thus fit this general rule.

Following the spring spawning the condition of the gonad in C. edule fluctuated, suggesting periodic gamete release during the summer months. However, the percentage of mature individuals involved never exceeded 25% of the total population. On the other hand, the initial spring spawning accounted for 68% of the population in 1968 and 44% in 1969. This period of major spawning took place over 15 days in 1968 and 18 days in 1969.

The gonad maturity of C. glaucum was maintained at a high level; above 55% of the total population from May 15th to July 11th (57 days) in 1968, and from May 10th until June 30th (51 days) in 1969. Spawning occurred in 50% of the population within 14 days in 1968 and in 54% of the population within 27 days in 1969 beginning on the dates stated. Thus in both the years studied the primary spawning period occurred

7 - 8 weeks later in C. glaucum than in C. edule.

Lebour (1938), as mentioned earlier studying the planktotrophic larva of C. edule, noted that metamorphosis and settlement of the spat occurred 4 - 5 weeks after fertilisation. Jones (Personal communication) found a similar length of planktonic life, in C. edule from the Dovey estuary, but Creek (1960), who also studied the Dovey cockles, records a larval life of only 2 - 3 weeks. Thus, assuming that the duration of larval life of the cockle is as long as 5 weeks it seems probable that settlement occurs in C. edule before the major spawning period of C. glaucum. This difference in the peak spawning period of the two cockles is reflected in the size of the first winter growth ring of the shell. The size of this ring in differently aged cockles is drawn up on table 11. Clearly the first year cockles of C. edule are larger than those of C. glaucum.

As the quantity of food available is greatest in spring, the larvae of C. edule can benefit from this high level of food abundance, whereas those of C. glaucum must enter the plankton during the summer period when food is normally less plentiful.

By combining the data for both sexes, an overall impression of gonad maturity of the two cockles can be compared.

Distribution of mature individuals of each sex in the two cockles

The percentage mature males and females (i.e. Grades III and IV) of each sample are shown in tables 9 and 10 and expressed graphically in figure 2.

These show that in both cockles, the males remain more mature than females throughout both spawning seasons. The greatest disappearance of

Table 9. Distribution of gonad maturity categories for C. edule during the survey 1968 - 1969.

The percentage of each grade has been calculated separately for each sex.

	FEMALES.								MALES.						TOTAL FEMALE.		TOTAL MALE.		INDETERMINATE		TOTAL NUMBER IN SAMPLE.
Date of collection	GRADE IV		GRADE III		GRADE II		GRADE I		GRADE IV		GRADE III		GRADE II								
	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	
5. 5.68	2	9	4	19	8	36	8	36	1	4	6	48	6	48	22	59	13	36	2	5	37
10. 5.68	7	32	9	41	6	27	-	-	4	50	2	25	2	25	22	73	8	27	-	-	30
15. 5.68	10	71	1	7	3	22	-	-	16	80	3	15	1	5	14	40	20	60	-	-	34
22. 5.68	2	5	15	38	10	25	13	32	8	22	19	50	11	28	40	45	38	43	11	12	89
30. 5.68	-	-	-	-	14	54	12	46	-	-	19	56	15	44	26	30	34	39	27	31	87
6. 6.68	-	-	9	17	33	64	10	19	-	-	19	40	28	60	52	39	47	36	33	25	131
13. 6.68	-	-	4	10	29	72	7	18	1	3	24	63	13	34	40	47	38	45	7	8	85
26. 6.68	-	-	2	7	21	75	5	18	2	5	20	54	15	41	28	36	37	48	12	16	77
11. 7.68	-	-	4	21	3	16	12	63	3	4	31	42	40	54	19	19	74	74	7	7	100
25. 7.68	-	-	3	14	10	48	8	38	-	-	9	31	20	69	21	40	29	55	3	5	53
8. 8.68	-	-	-	-	4	14	25	86	-	-	6	22	21	78	29	46	27	43	7	11	63
22. 8.68	-	-	-	-	9	28	23	72	-	-	15	38	24	62	32	36	39	44	18	20	89
11. 9.68	-	-	-	-	3	13	20	87	-	-	1	6	16	94	23	43	17	32	13	25	53
26. 9.68	-	-	-	-	8	40	12	60	1	4	7	29	16	67	20	40	24	48	6	12	50
24.10.68	-	-	-	-	14	33	28	67	-	-	2	5	38	95	42	34	40	32	42	34	124
21.11.68	-	-	14	13	30	28	62	59	-	-	4	12	30	88	106	54	34	17	58	29	198
21.12.68	-	-	-	-	10	15	58	85	-	-	-	-	18	100	68	44	18	11	72	45	158
22. 1.69	-	-	-	-	2	5	39	95	-	-	-	-	9	100	41	43	9	9	46	48	96
8. 3.69	-	-	-	-	3	8	36	92	-	-	1	10	9	90	39	57	10	15	19	28	68
7. 4.69	-	-	-	-	10	20	39	80	-	-	-	-	16	100	49	49	16	16	34	35	99
22. 4.69	-	-	3	8	15	38	21	54	-	-	1	8	11	92	39	54	12	16	22	30	74
4. 5.69	2	9	6	27	11	50	3	14	15	54	5	18	8	28	22	41	28	53	3	6	53
10. 5.69	5	45	3	27	2	18	1	10	14	56	10	40	1	4	11	28	25	64	3	8	39
18. 5.69	-	-	8	40	9	45	3	15	5	25	12	60	3	15	20	48	20	48	2	4	42
29. 5.69	-	-	-	-	4	40	6	60	2	10	8	40	10	50	10	29	20	59	4	12	34
5. 6.69	-	-	3	25	7	58	2	17	3	21	6	43	5	36	12	41	14	48	3	11	29
15. 6.69	-	-	2	7	18	64	8	29	-	-	9	56	7	44	28	61	16	35	2	4	46
30. 6.69	-	-	2	20	6	60	2	20	-	-	6	46	7	54	10	25	13	32	17	43	40
14. 7.69	-	-	3	23	7	54	3	23	-	-	8	44	10	56	13	39	18	54	2	7	33
27. 7.69	-	-	1	10	10	90	-	-	3	19	8	50	5	31	11	35	16	52	4	13	31
19. 8.69	1	7	2	13	10	67	2	13	-	-	4	27	11	73	15	45	15	45	3	10	33
10. 9.69	-	-	-	-	8	50	8	50	-	-	2	13	14	87	16	46	16	46	3	8	35

Table 10. Distribution of gonad maturity categories for C. glaucum during the survey 1968 - 1969.

The percentage of each grade has been calculated separately for each sex.

Date of collection	FEMALES. GRADE IV Nos.	%	GRADE III Nos.	%	GRADE II Nos.	%	GRADE I Nos.	%	MALES. GRADE IV Nos.	%	GRADE III Nos.	%	GRADE II Nos.	%	TOTAL FEMALE. Nos.	%	TOTAL MALE. Nos.	%	INDETERMINATE Nos.	%	TOTAL NUMBER IN SAMPLE.
5. 5.68	1	8	3	23	7	54	2	15	2	10	2	10	16	80	13	33	20	52	6	15	39
10. 5.68	2	34	2	33	2	33	-	-	4	27	8	53	3	20	6	27	15	69	1	4	22
15. 5.68	8	73	2	18	1	9	-	-	5	82	2	28	-	-	11	61	7	39	-	-	18
22. 5.68	16	50	10	31	3	9	3	9	12	44	9	33	6	23	32	49	27	42	6	9	65
30. 5.68	16	50	10	31	4	12	2	7	21	47	15	33	9	20	32	30	45	41	31	29	108
6. 6.68	4	14	16	57	7	25	1	4	2	8	18	72	5	20	28	40	25	37	16	23	69
13. 6.68	5	11	34	76	2	4	4	9	3	8	30	75	7	18	45	49	40	42	7	8	92
26. 6.68	30	48	22	35	10	16	1	1	16	33	24	49	9	18	63	50	49	38	15	12	127
11. 7.68	-	-	14	39	21	58	1	3	-	-	40	71	16	29	36	37	56	59	4	4	96
25. 7.68	-	-	-	-	27	71	11	29	-	-	4	13	20	87	38	58	24	37	3	5	65
8. 8.68	-	-	1	3	13	45	15	52	-	-	4	15	23	85	29	42	27	40	12	18	68
22. 8.68	-	-	-	-	-	-	20	100	-	-	2	12	14	88	20	22	16	17	56	61	92
11. 9.68	-	-	1	4	5	21	18	75	-	-	1	10	9	90	24	39	10	16	28	45	62
26. 9.68	-	-	-	-	2	8	22	92	-	-	4	20	16	80	24	30	20	25	36	45	80
24.10.68	-	-	-	-	-	-	21	100	-	-	-	-	20	100	21	15	20	14	98	70	139
21.11.68	-	-	-	-	-	-	75	100	-	-	4	25	12	75	75	38	16	8	108	54	199
21.12.68	-	-	-	-	-	-	46	100	-	-	-	-	2	100	46	30	2	1	104	68	152
22. 1.69	-	-	-	-	-	-	19	100	-	-	-	-	1	100	19	18	1	1	85	81	105
8. 3.69	-	-	-	-	-	-	30	100	-	-	-	-	1	100	30	41	1	1	43	58	74
7. 4.69	-	-	-	-	-	-	59	100	-	-	-	-	-	-	59	43	-	-	80	57	139
22. 4.69	-	-	-	-	2	20	8	80	-	-	-	-	8	100	10	19	8	14	36	67	54
4. 5.69	9	26	9	26	10	28	7	20	23	60	10	26	5	14	35	38	38	41	19	21	92
10. 5.69	5	62	1	13	2	25	-	-	14	82	2	12	1	6	8	29	17	60	3	11	28
18. 5.69	15	75	3	15	1	5	1	5	8	89	-	-	1	11	20	65	9	29	2	6	31
29. 5.69	6	26	9	39	2	9	6	26	6	27	14	64	2	9	23	49	22	47	2	4	47
5. 6.69	11	65	3	18	2	12	1	5	8	57	5	36	1	7	17	49	14	40	4	11	35
15. 6.69	11	30	18	49	6	16	2	5	-	-	15	71	6	29	37	64	21	36	-	-	58
30. 6.69	11	44	9	36	4	16	1	4	11	29	20	53	7	18	25	39	38	59	1	2	64
14. 7.69	2	9	7	32	9	41	4	18	1	4	12	44	14	52	22	45	27	55	-	-	49
27. 7.69	-	-	1	6	13	81	2	13	-	-	8	47	9	53	16	48	17	52	-	-	33
19. 8.69	-	-	9	47	9	47	1	6	1	5	13	56	9	39	19	44	23	54	1	2	43
10. 9.69	-	-	2	8	16	67	6	25	-	-	3	25	9	75	24	56	12	28	7	16	43

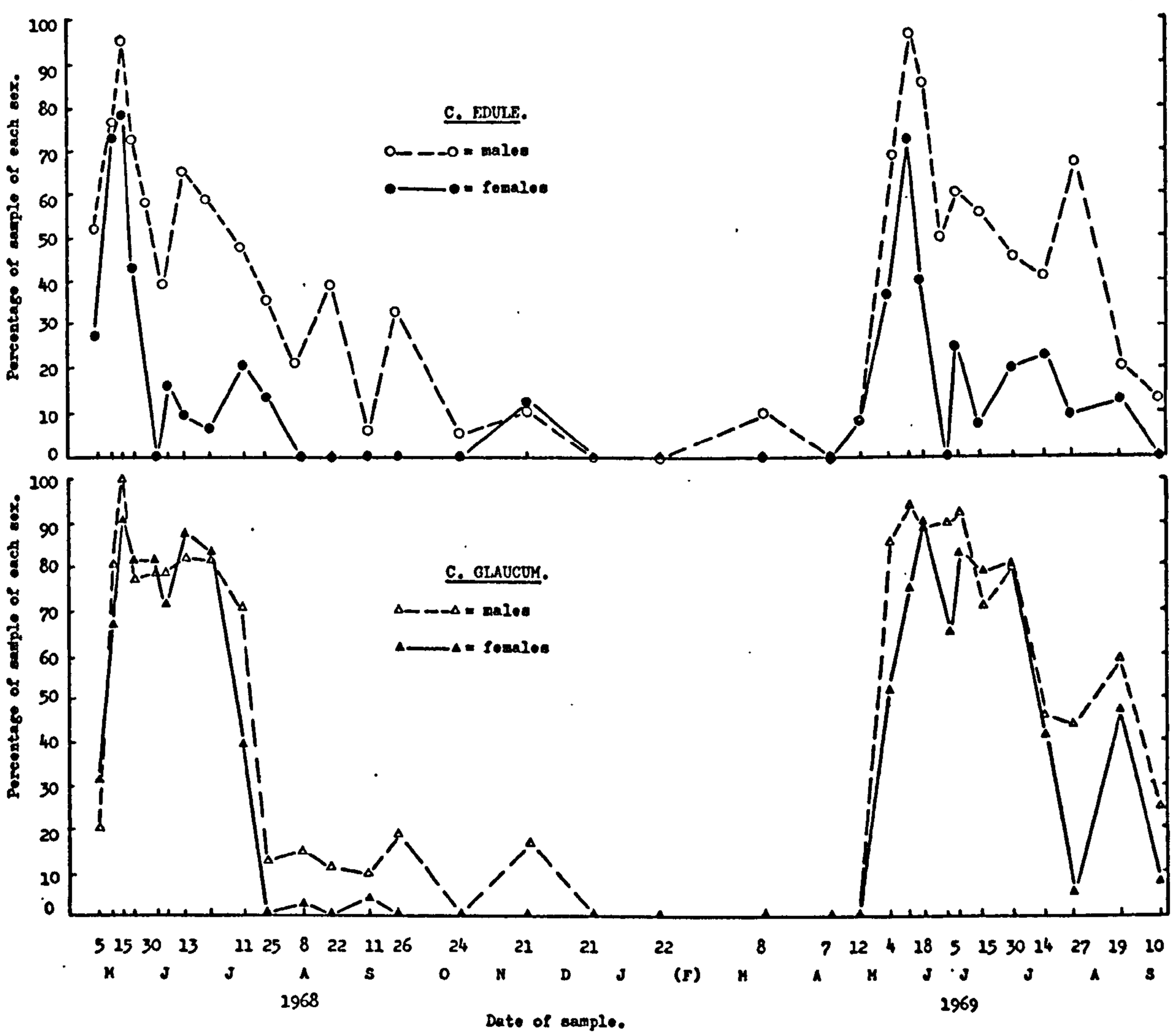


Fig 2 - Comparison of the maturity of male and female Cerastoderma collected from the Crouch mixed population between May 1968 and September 1969.

spermatazoa from the testes occurred after the females has spawned. In C. edule it was particularly noticeable that the males are riper than the females during the summer months. Also, in this cockle there appears to be fluctuations in the ripeness of the male, perhaps indicating a periodicity in spawning. Thus, in C. edule there was a slight increase in the number of mature females in November which suggests a second smaller spawning in late autumn. Certainly developing ova were present in C. edule during August 1968.

In C. glaucum the maturation and spawning of the males followed the females very closely. Syncronised spawning thus seems to be better co-ordinated in this cockle than in C. edule.

Distribution of mature females in the two cockle populations

It was noted in the experiments investigating the possibility of hybridization that the maturity of the female ova was particularly important for successful fertilisation. The percentage of mature females (i.e. Grades III and IV) of both cockles have been plotted in figure 3. From this graph it is apparent that liberation of ova occurred over periods of 15 and 19 days in C. edule and 29 and 27 days in C. glaucum in the two spawning seasons. This also suggests that synchronization in spawning is a feature of both cockles. During the spring spawning of C. edule there is correspondingly a very slight decrease in the maturity of C. glaucum. However, the percentage of mature C. glaucum then increases and remains at a high level until the July summer spawning. From the experiments investigating fertilisation (see earlier) it seems that, although the gonads appeared to be mature in C. glaucum during May and June the gametes were not ready for spawning. The number of days between the completion of spawning in C. edule and

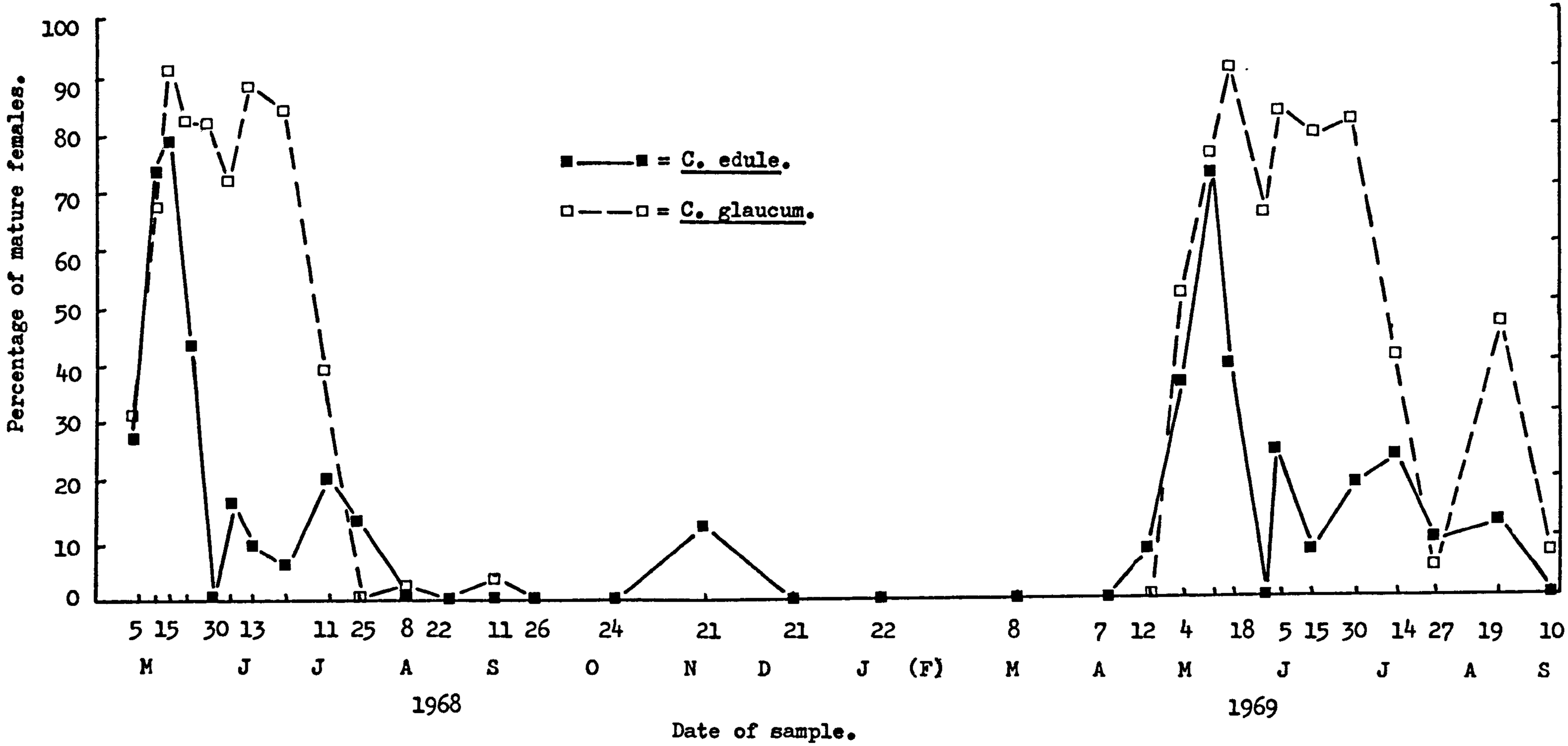


Fig 3 - Comparison of mature females of C.edule and C.glaucum collected from the Crouch mixed population from May 1968 until September 1969.

Table 11.

Average shell depth mm's of first winter growth ring in both Cerastoderma of various ages collected from the Crouch mixed cockle population.

1)C.edule.

Numbers examined.	Age of cockle (number of winter rings)	Average depth of first ring in mm's
10	1	16.7
10	2	17.3
15	3	16.1
19	4	16.5
15	5	13.8
10	6	15.6
10	7	11.9
Total examined 89	-	Total average= 15.5mm's

2) C. glaucum

10	1	9.4
23	2	10.7
46	3	10.3
20	4	11.1
14	5	8.4
10	6	6.7
Total examined 123	-	Total average = 9.9mm's

C. glaucum was 56 days in 1968 and 58 days in 1969. The spawning of females of these two cockles therefore differed by 7 weeks in animals collected from the same tidal level.

Reproductive state of other populations of Cerastoderma

Various other populations of Cerastoderma were examined occasionally throughout 1968 and 1969. The gonad state of these cockle populations is recorded in table 12.

This shows that the percentage of indeterminate individuals of the two cockles collected from the Roach estuary and from the Fleet, Dorset, during the summer and autumn of 1968 was similar to that found in the Crouch populations.

Rapid gametogenesis occurred in the Southend population of C. edule, leading to the onset of spawning before May 18th 1968. This was similar to the C. edule in the Crouch. The percentage of spent individuals overwintering was higher in the Southend C. edule than in the Crouch population of this cockle, and this is also reflected to a lesser extent in the Salcombe, Devon and Tollesbury, Essex cockles.

The percentage of spent individuals of C. glaucum collected in January from the New England Creek lagoon, Essex is also as high as in the Crouch C. glaucum. This suggests some uniformity in the nature of the breeding cycles in both lagoonal and shore populations of C. glaucum. The lagoon C. glaucum populations also appear to undergo rapid gametogenesis, as there were no indeterminate individuals remaining on the 21st April 1969 at Widewater lagoon, Sussex. This is in direct contrast to the Crouch C. glaucum, where 67% of the population were undifferentiated at this time. Thus it appears that gametogenesis occurs earlier in lagoon populations in comparison with shore populations,

Table 12

Reproductive state of various cockle populations examined during 1968 & 1969.

Locality.	Cockle type.	Date & size of sample.	Predominant grades of males.	Predominant grades of females.	Percentage of indeterminate individuals in sample.
The Fleet entrance, Portland, Dorset.	C.edule	12. 8.68,31	11-111	1-11	20
The Fleet, "	C.glaucum	" 64	11-111	1-11	40
River Roach,Essex.	C.edule	9.10.68 36	11	1	33
" " "	C.glaucum	" 23	11	1	64
Southend,Essex,	C.edule	26. 1.69 100	11	1	76
" "	"	27. 2.69 85	11developing.	1	68
" "	"	18. 5.69 46	111-1V ripe.	11-111	0
Salcolme estuary, Devon.	C.edule	25. 3.69 17	11	1	50
Portsmouth, Hants.	C.edule	27. 5.69 22	11-111	11	0
(" "	C.glaucum	" 3	111	111	0)
Wexford Harbour, Eire.	C.edule	13. 8.69 18	111-1V	11-111	0
Tollesbury, Essex.	C.edule	19.10.69 28	11	1	50
New England Creek	C.glaucum	26. 1.69 107	-	1	75
Widewater, Sussex.	"	21. 4.69 8	1V ripe	1V	0
Gosport, Hants.	"	7. 6.69 30	11-111	1-11	2
Sheerness,Kent.	"	17. 6.69 72	11	1-11	0
Widewater, Sussex.	"	21. 7.69 21	-	1	90
Sheerness,Kent.	"	25. 7.69 11	11-111	1	60

presumably because of the higher water temperatures that occur in spring in these localities.

The whole C. glaucum population at Widewater was mature by the 21st April 1969, initial spawning would, therefore, be expected soon after this date. Spawning had occurred in Gosport lagoon populations before the 7th June 1969, and in Sheerness lagoon population, Kent it had occurred before the 17th June 1969. When the Widewater population was sampled again on the 21st July 1969 the whole population was spent. In contrast, the majority of the Crouch C. glaucum population, although apparently mature by the 10th May 1969 did not commence spawning until the 30th June 1969. Even in September the percentage of spent C. glaucum from the Crouch population was only 16%, whereas 90% and 60% of the Sheerness and Widewater populations respectively were spent by the end of July.

Thus the lagoon populations of C. glaucum undergo very rapid gametogenesis in the spring and spawn earlier during the summer months than the Crouch shore population of this cockle.

Relationship between environmental temperature and spawning in the two Cerastoderma

The numerous physical and biological variables of the environment that control the reproductive cycles of marine invertebrates have been reviewed elsewhere (Giese, 1959). Temperature has long been recognised as one of the most important environmental parameters, but recent information suggests that other features also play a critical role in the co-ordination of spawning.

It has been stated by Orton (1920) that many animals begin to breed either at a definite temperature, which is a physiological constant

for that species, or at a definite temperature change. This is undoubtedly an oversimplification as many invertebrates, such as C. edule, seem to spawn regularly or irregularly within a limited temperature range. Korringa (1957) analysed the data available for Ostrea edulis, relating water temperature to spawning, and has shown that the fine co-ordination of spawning is dictated by factors other than temperature.

Nevertheless, Battle (1933) suggested that the spawning of Macoma balthica was induced by high temperatures of the mud flat habitat during new moon neaps when the shore was exposed at midday. Korringa (1947) criticised this conclusion, pointing out that the flats were also exposed daily during full moon neaps. Giese (1969) correlated the gonad index of the chiton Katharina tunicata with water temperature over a 10 year period. He concludes in Webber & Giese (1969) that there is no correlation between continual increase in water temperature and gonad development. Nevertheless, spawning of this chiton over this 10 year period always occurred between 13.5 and 14.5°C.

The relationship between environmental water temperature and air temperature with spawning of the two Cerastoderma over successive years is shown in figures 4 and 5. In C. edule there appears to be correlation of spawning with water temperature, spawning occurring at 13.2°C. in 1968 and 12.9°C in 1969. In C. glaucum no correlation seems possible with either water or air temperatures. The wide fluctuations and differences between air and water temperatures of successive years is pronounced in this data and emphasizes the need to determine other factors which influence the synchronisation of spawning.

Fig 4 - Values of mean maximum air and water temperatures for Burnham - on - Crouch during the 1968 spawning season, related to spawning periods of the two cockles.

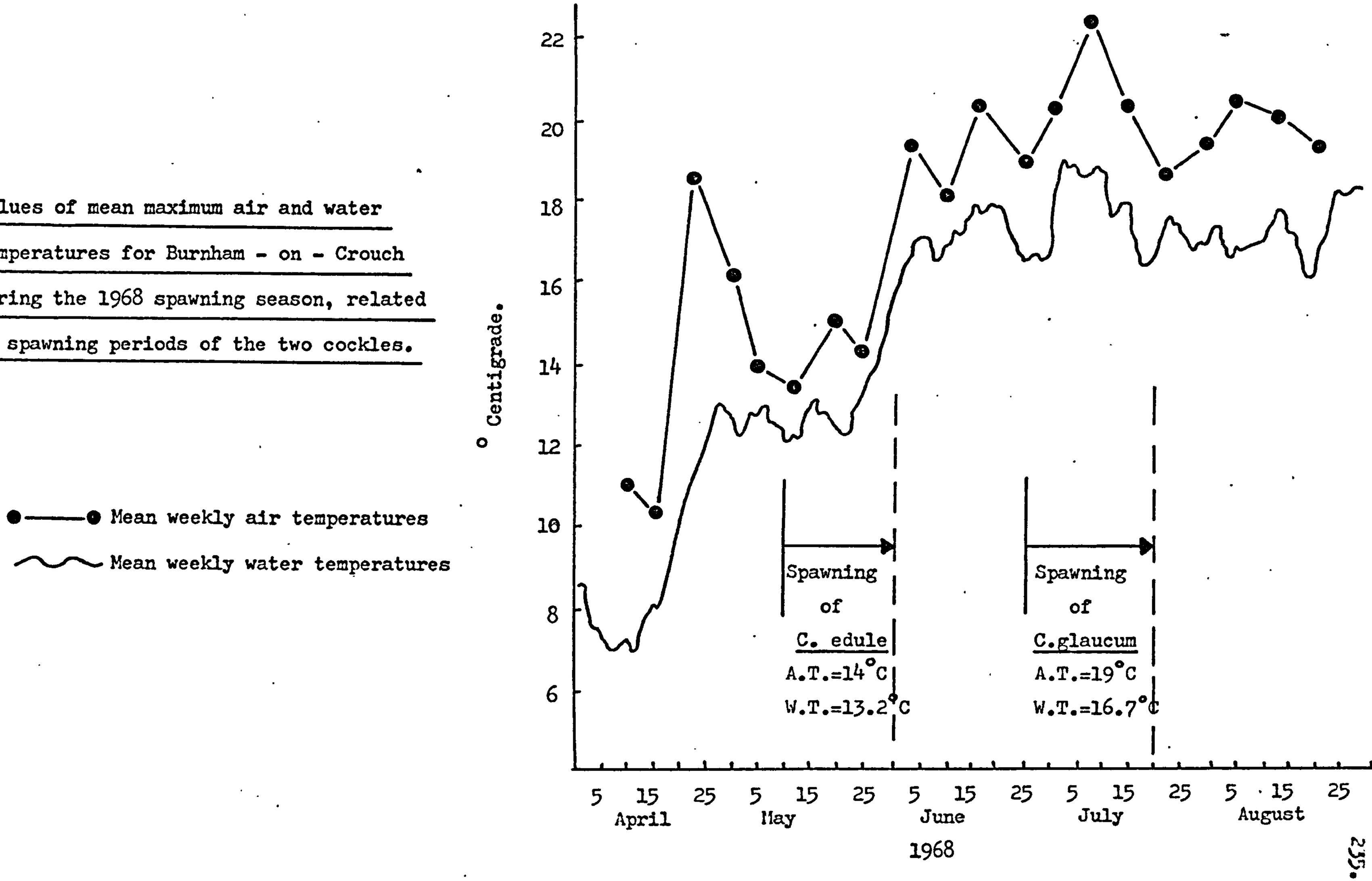
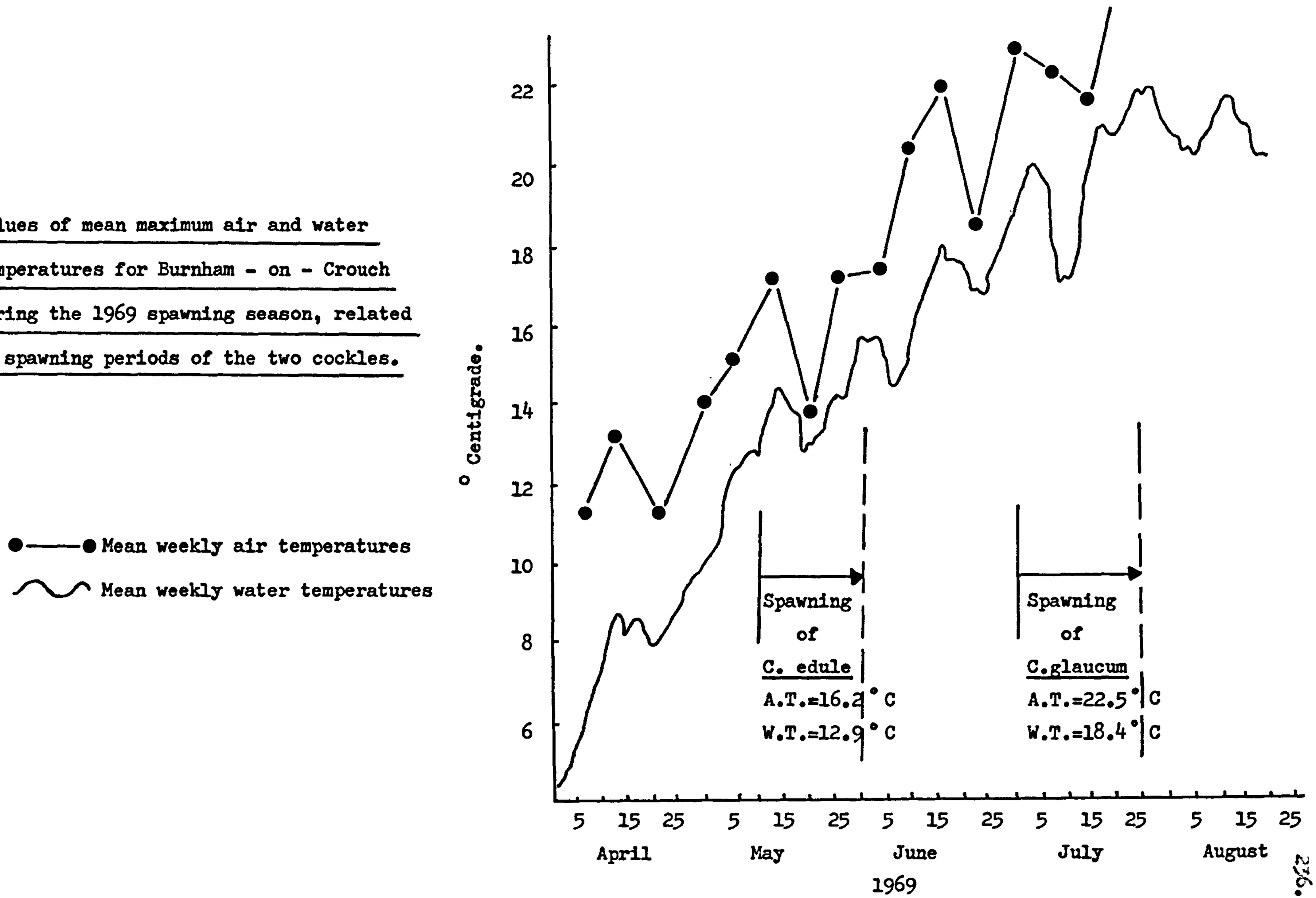


Fig 5 - Values of mean maximum air and water temperatures for Burnham - on - Crouch during the 1969 spawning season, related to spawning periods of the two cockles.



Discussion

The reproductive cycle of lamellibranchs usually takes the following form: a progressive development from the animal in a condition in which the gonads are undifferentiated, through differentiation of the gonad, (gametogenesis and maturation of the gametes), to spawning either partially or completely of the gametes and a return to one of these earlier stages. In many lamellibranchs, e.g. Mya arenaria, (Coe & Turner, 1938); Venerupis straminae, (Quayle, 1943); V. pullustra, (Quayle, 1948); Venus striatula (Ansell, 1961); adult Mercenaria mercenaria, (Loosanoff, 1937; Porter, 1964); Cyprina islandica, (Loosanoff, 1953); and Macoma balthica, (Caddy, 1967), a major redevelopmental or initial gametogenetic period occurs immediately after spawning. Here the gametes develop to varying degrees in the autumn and are maintained over winter at this stage, a second gametogenic period of development occurring in the following spring. As has been shown earlier, this type of gonad development is not displayed by the Cerastoderma.

A second category of bivalves undergo a period of fattening following summer spawning. Thus, Mytilus edulis (Chipperfield, 1953; Seed, 1969); Mytilus edulis planulatus (southern hemisphere sub-species of M. edulis) (Wilson and Hodgkin, 1967); and oysters, (Loosanoff, 1963), accumulate glycogen and fat in the connective tissue of the gonad and mantle during the autumn prior to gametogenesis and spawning occurs in late winter or early spring. A loss of sexuality accompanies the prolific development of the interfollicular tissue during the autumn. Cockles are, therefore, similar to the above group of lamellibranchs in that gametogenesis does not occur immediately after spawning. However, in contrast to mussels and oysters the loss of sexuality is not

accompanied by development of the interfollicular gonadial tissue.

Although within the Cerastoderma, gametogenesis is initiated in some individuals during the cold winter months, it is during the spring months of March and April that precocious gonad development occurs. Thus, in cockles, as in some other bivalves, e.g. Mytilus edulis, Ostrea edulis and Tivela stultorum, (Herrington, 1930), gametogenesis immediately precedes spawning.

Ansell and Loosmore (1963) recognised that in Mercenaria mercenaria development of the gonad only took place when sufficient food was available. Thus, cockles like the above clams, reach their peak of condition immediately before and during the spawning season.

One of the simplest reproductive patterns found in marine invertebrates is 'broadcast ferilisation', (Webber & Giese, 1969), where gametes are released by spawning into the environment and external fertilisation occurs. Larvae with a long pelagic existence could then be spread far and wide by tidal streams, settlement possibly occurring far from the adult location. Nevertheless, the importance of co-ordinated spawning at favourable times should not be underestimated as an agent which assists in reproductive isolation.

Marine invertebrates, especially of temperate waters, exhibit synchronised gamete release within populations, (Thorson, 1946). Young (1946) studying the reproduction of Mytilus californianus showed that a marked difference in times of spawning occurred between mussels from different localities. It has also been shown by Fritzenmeyer (1962), Ropes and Stickney (1965) and Shaw (1964) that the annual gonad cycle of Mya arenaria varies from locality to locality. The influence of the environment upon control of reproduction is reflected by the longer and earlier spawning seasons in southern populations of the same species,

e.g. Mercenaria mercenaria (Porter, 1964). Similarly, Korringa (1957) considers that various races, varieties or genotypes of the European oyster Ostrea edulis occur in Northern Europe, which spawn at different temperatures, and he also applies this theory to the American oyster Crassostrea virginica. Finally, it has been recently shown by Webber and Giese (1969) that the intertidal abalone Haliotis cracheroidii collected from two populations separated by only seven miles, spawn six weeks apart. As the shore temperatures influencing these two populations were probably very similar, this example indicates that co-ordination of spawning is far from simple and is probably dictated by the co-ordination of a variety of environmental factors. This complexity of co-ordination of spawning can thus be looked upon as an important factor that might facilitate speciation in marine invertebrates.

Certainly it has been shown earlier that the time of spawning of C. edule varies from year to year (see previous studies on the reproductive cycles of the Cerastoderma). During the time of this survey an investigation into the histological nature of gametogenesis in the Cerastoderma was being conducted elsewhere by Kingston. He reports, Kingston (Personal communication) that the spring spawning of C. edule in 1968, collected from Littlestone, East Kent occurred between May 26th and June 26th, whilst the spawning of the Crouch C. edule was initiated by May 15th. It could be suggested that temperature (and perhaps phytoplankton abundance) may have been greater in the upper Crouch estuary than in the open sea off Kent, and this could account for the earlier spawning in the Essex cockles. If two populations apparated geographically and/or subjected to different environmental conditions spawn at different times, then reproductive isolation between adjacent populations becomes possible.

Thus, in marine invertebrates, freely releasing gametes into the sea, speciation is probably equally as possible as it is in viviparous or oviparous species. By the complex process of synchronous spawning reproductive isolation can be achieved between populations, and the success of this is reflected in the enormous diversity of invertebrates reproducing in this manner.

It has been noted earlier that the common cockle, C. edule after an initial spring spawning, releases gametes periodically during the summer. The significance of this to the species is debatable and has been noted elsewhere in other invertebrates (Giese 1959). On the event of catastrophic failure of the spring spawning the evolutionary value of spawning during the summer is obvious, as some larvae will then have a chance to survive. This reasoning is supported by the fact that spawning can fail for several years in succession. Thorson (1950) showed that lamellibranchs which possess a long pelagic larval life fluctuated widely in numbers whereas examples with short planktonic existence were much more stable in numbers over several years. Certainly, in C. edule dominance of year classes is a cyclical process, successful year classes often being separated by several years of poor settlement. Protracted summer spawning of small numbers of gametes may be regarded as an insurance policy to compensate for possible failures of the synchronised initial spring spawning.

Conclusion

It has thus been shown in C. edule and C. glaucum from the Crouch mixed cockle population, that the gametes are spawned at separate times. Thus, in a common environment, the control of synchronisation of spawning differs in the two cockles. This would not be consistent with

the theory that the cockles are merely varieties of a single genetic stock, but suggest that the relationship is more established.

The presence of reproductive isolation in the mixed cockle population could indicate either incipient divergence between the cockles, or that the population is an example of convergence subsequent to divergence. Because both C. glaucum and C. edule are widely distributed (Russell, 1969), the Crouch mixed cockle population cannot be regarded as an example of initial separation between the two cockle types. It would appear that the relationship between C. edule and C. glaucum is an excellent example of a recently speciated species pair, (Mayr, 1949). Divergence of the two cockles is reflected in their ecological preferences, C. glaucum inhabiting stagnant, saline lagoons whilst C. edule occurs intertidally. During this separation it could be envisaged that differences in co-ordination of reproduction between the two cockles have become established. Thus, in the Crouch mixed population, where the two cockles have come together, reproductive isolation has been maintained, and the two cockles retain their genetic individuality. The Cerastoderma can thus be looked upon as another very closely related species pair, which follow Mayr's theory of allopatric speciation.

REFERENCES

ANSELL, A.D., 1961. The development of the primary gonad in Venus striatula (da Costa). Proc. Malacol. Soc. Lond. Vol. 34 (5), pp. 243-247.

ANSELL, A.D. & LOOSMORE, F.A., 1963. Preliminary observations on the relationship between growth, spawning and conditions in experimental colonies of Venus mercenaria L. J. cons. int. Explor. Mer. Vol. 28, pp. 285-290.

BARKER-JØRGENSEN, C., 1946. Lamellibranchiata in 'Reproduction and larval development of Danish marine bottom invertebrates' (by G. Thorson) pp. 277-311. Medd. Fra. Komm. Dan. Fisk-og.Havunders. Serie: Plankton, Bind 4. N.R.1.

BATTLE, H.I., 1933. Rhythmic sexual maturity and spawning of certain bivalve mollusks. Contrib. Can. Biol. Fisheries, N.S. Vol. 7, (20) pp. 257-276.

BENNETT, J. & GIESE, A.C., 1969. The annual reproductive cycle and nutritional cycles in two western sea urchins. Biol. Bull. mar. biol. Lab., Woods Hole. Vol. 109, pp. 226-237.

BLACKMORE, D.T., 1969. Studies of Patella vulgata (L.) I. Growth, reproduction and zonal distribution. J. exp. mar. Biol. Ecol. Vol. 3, pp. 200-213.

BOYDEN, C.R., 1969. Ecology of the cockle Cardium glaucum Bruguière. Essex Nat. Vol. 32(3), pp. 223-226.

CADDY, J.F., 1967. Maturation of gametes and spawning in Macoma balthica (L.). Canad. J. of Zool. Vol. 45, pp. 955-965.

CHAVAN, A., 1945. Essai de correlation entre les varietes du Cardium edule. Bull. Mus. Hist. Nat. Paris, series 2e. Vol. 17, pp. 121-135.

CHIPPERFIELD, P.N.J., 1953. Observations on the breeding and settlement of Mytilus edulis L. in British waters. J. mar. biol. Ass. U.K. Vol. 32, pp. 449-476.

COE, W.R., 1934. Alteration of sexuality in oysters. Am. Nat., Vol. 68, pp. 236-251.

COE, W.R., 1936. Sequence of functional sexual phases in Teredo. Biol. Bull., Vol. 71, pp. 122-32.

COE, W.R. & TURNER, H.J., Jr., 1938. Development of the gonads and gametes in the soft-shell clam (Mya arenaria), J. Morph. Vol. 62 (1), pp. 91-111.

COEN, J.S., 1915. Nota sui Cardium della sezione Cerastoderma. Atti. Sci. Veneto-Trentino, serie terza, Vol. 8, pp. 54-62.

CREEK, G.A., 1960. The development of the lamellibranch Cardium edule L. Proc. Zoo. Soc. Lond. Vol. 135, pp. 243-260.

DAVIS, H.C. & CHANLEY, P.E., 1956. Spawning and egg production of oysters and clams. Biol. Bull. mar. biol. Lab., Woods Hole, Vol. 110, pp. 117-128.

EISMA, D., 1965. Shell Characteristics of Cardium edule (L.) as indicators of salinity. Neth. J. of Sea Res., Vol. 2, pp. 493-540.

GALTSOFF, P.S., 1956. 'The American oyster Crassostrea virginica' - G. melin. Bull. Fish. and Wildlife Service, Vol. 64.

GIESE, A.C., 1959. Annual reproductive cycles of marine invertebrates. Ann. Rev. Physiol. Vol. 21, pp. 547-576.

GIESE, A.C., 1969. A new approach to the biochemical composition of marine invertebrates. Oceanogr. mar. Biol. Ann. Rev. Vol. 5, pp. 159-186.

GROSSU, A.V., 1961. Les Variations de Cardium edule L. dans la mer Noire. Hydrobiologia Bucureşti, Vol. 3, pp. 177-191.

HANCOCK, D.A., 1969 (Personal communication, Unpublished data).

HERRINGTON, W.C., 1930. The Pismo clam. Fish. Bull. California Vol. 18, pp. 1-69.

HØPNER-PETERSEN, G., 1958. Notes on the growth and biology of the different Cardium species in the Danish brackish water areas. Medd. Dan. Fisk-og.Havunders, Ny serie, Vol. 2, No. 22, pp. 1-31.

JOHNSTON, J., 1899. L.M.B.C. Memoirs II. Cardium. Dobb & Co., Liverpool.

JONES, A., 1970. (personal Communication).

KINGSTON, P., 1970. (Personal communication).

KORRINGA, P. 1947. Relations between moon and periodicity in the breeding of marine animals. Ecol. Monographs, Vol. 17, pp. 347-381.

KORRINGA, P., 1957. Water temperature and breeding throughout the geographical range of Ostrea edulis. L'Année Biol. Vol. 33, pp. 1-17.

KRISTENSEN, I., 1957. Differences in the density and growth in a cockle population in the Dutch Walden Sea. Arch. Néerl. de Zool., Vol. 12, pp. 351-453.

LEBOUR, M.V., 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae. J. mar. biol. Ass. U.K., Vol. 23, pp. 119-145.

LOOSANOFF, V.L., 1937. Seasonal gonadal changes of adult clams. Venus mercenaria (L). Biol. Bull. mar. biol. Lab., Woods Hole, Vol. 72, pp. 406-416.

LOOSANOFF, V.L., 1942. Seasonal gonadal changes in the adult oyster of Ostrea virginica of Long Island Sound. Biol. Bull. mar. biol. Lab., Woods Hole. Vol. 32, pp. 195-206.

LOOSANOFF, V.L., 1953. Reproductive Cycle in Cyprina Islandica. Biol. Bull. mar. Lab., Woods Hole, Vol. 104, pp. 146-155.

LOOSANOFF, V.L., 1963. Gametogensis and spawning of the European oyster O. edulis in waters of Maine. Biol. Bull. mar. biol. Lab., Woods Hole, Vol. 122, pp. 86-94.

LOOSANOFF, V.L. & ENGLE, J.B., 1942. Accumulation and discharge of spawn by oysters living at different depths. Biol. Bull. mar. biol. Lab., Woods Hole, Vol. 82, pp. 413-422.

MARS, P., 1951. Essai d'interpretation des formes generalement groupes sous le nom de Cardium edule. Linne. Bull. Mus. Hist. Nat. Marseilles, Vol. 11, pp. 1-31.

MAUZEY, K.P., 1966. Feeding behaviour and reproductive cycles in Pisaster ochraceus. Biol. Bull. mar. Lab., Woods Hole, Vol. 131, pp. 127-144.

MAYR, E., 1949. Speciation and selection. Proc. Amer. Phil. Soc., Vol. 93, pp. 514-519.

MAYR, E., 1957. Species concepts and definitions In. E. Mayr Ed. 'The species problem' (Amer. Assoc. Adv. Sci. Publ. No. 50), pp. 1-22.

MAYR, E., 1963. 'Animal species and Evolution'. Belknap Press, Cambridge, Massachusetts. Harvard Univ. Press, London, Oxford Univ. Press.

NELSON, Th.C., 1928. Relation of spawning of the oyster to temperature. Ecology 9(2), pp. 145-154.

ORTON, J.H., 1920. Sea temperature, breeding and distribution of marine animals. J. mar. Biol. Ass. U.K. Vol. 12, pp.339-366.

ORTON, J.H., 1926. On the rate of growth of Cardium edule, part I. Experimental observations. J. mar. biol. Ass. U.K. Vol. 14, pp. 239-279.

ORTON, J.H., 1933. Summer Mortality of cockles on some Lancashire and Cheshire Dee Beds in 1933. Nature, Vol. 132, pp. 314-315.

ORTON, J.H., et al. 1956. Studies on the biology of limpets. II Breeding of Patella vulgata L. in Britain. J. mar. biol. Ass. U.K. Vol. 35, pp. 149-176.

PFITZENMEYER, H.T., 1962. Periods of Spawning and Settling of the soft-shelled Clam, Mya arenaria at Solomons, Maryland. Chesapeake Sci., Vol. 3, pp. 114-120.

PORTER, H.J., 1964. Seasonal gonadal changes in adult clams, Mercenaria mercenaria (L.) in North Carolina. Proc. Nat. Shellf. Assoc. Vol. 55, pp. 35-52.

QUAYLE, D.B., 1943. Sex, gonad development and seasonal gonad changes in Paphia straminea.Conrad. J. Fisheries Res. Board. Can. Vol. 6(2) pp. 140-151.

QUAYLE, D.B., 1952. Structure and biology of the larva and spat of Venerupis pullastra (Montagu) Trans. Roy. Soc. Edinb. Vol. 62, pp. 255-297.

ROPES, J.W. & STICKNEY, A.P., 1965. Reproductive cycle of Mya arenaria in New England. Biol. Bull. mar. biol. Lab., Woods Hole, Vol. 128, pp. 315-327.

RUSSELL, P.J.C., 1969. Studies on the ecology distribution and morphology of the cockles Cardium edule L. and C. glaucum Bruguière. Ph.D. Thesis, London.

SEED, R., 1969. The Ecology of Mytilus edulis L. (Lamellibranchiata) on Exposed Rocky Shores. I Breeding and Settlement. Oceanologia (Berl.), Vol. 3, pp. 277-316.

SHAW, W.N., 1964. Seasonal gonadal changes in female soft-shell clams, Mya arenaria in the Tred. Avon River, Maryland. Proc. Nat. Shellfish Ass. Vol. 53, pp. 121-132.

THORSON, G., 1946. Reproductive and larval development of Danish Marine bottom invertebrates. Medd. Fra. Komm, Dan. Fisk-og Havunders Serie: Plankton, Vol. 4, N.R.1.

THORSON, G., 1950. Reproductive and larval ecology of marine bottom fauna. Bio. Rev. Vol. 25, pp. 1-45.

WEBBER, H.H. & GIESE, A.C., 1969. Reproductive cycle and gametogenesis in the black abalone Haliotis cracheroidii (Gastropoda : Prosobranchiata) Marine Biology, Vol. 4(2), pp. 152-159.

WILLIAMS, G.B., 1965. Studies on breeding in Spirorbis borealis Daudin (Polychaeta). Ph.D. Thesis, Section II, Univ. Coll. of North Wales.

WILSON, D.P. & ARMSTRONG, J.A.J., 1954. Biological differences between sea waters : Experiments in 1953. J. mar. biol. Ass. U.K., Vol. 33 pp. 347-360.

WILSON, B.R., & HOCKIN, E.P., 1967. A comparative account of the reproductive cycles of five species of marine mussels (Bivalvia Mytilidae) in the vicinity of Freemantle, W. Australia. Aust. J. mar. Freshwat. Res. Vol. 18, pp. 175-203.

WINKWORTH, R., 1932. The British marine Mollusca. J. Conch., Vol. 19, pp. 211-252.

WRIGHT, F.S., 1926. A report on the cockle beds and the cockle industry of England and wales. Min. Agric. Fish., Fish Invest. Ser. 2, Vol. 9(5), pp. 1-45.

YOUNG, R.T. 1946. Spawning and settling season of the mussel Mytilus californianus Ecology. Vol. 27, pp. 354-363.

SECTION - VII

SECTION VII

A COMPARATIVE INVESTIGATION INTO THE SYMBIONT FAUNA OF THE COCKLES CERASTODERMA EDULE (L.) AND CERASTODERMA GLAUCUM (POIRET)

Introduction

Host specificity of digenetic trematodes has been considered to be due either to physiological or ecological factors, (Baer, 1951; Hargis, 1957; Heynemann, 1960; Wright, 1960; Llewellyn, 1965). Further, it is generally accepted that a high degree of 'phylogenetic' host specificity occurs in the selection of the first intermediate molluscan host, whilst the specificity at the definitive host level is more ecologically dictated and is generally less specific.

Kendall (1964) notes that the complex systematics of some molluscs, especially the snails, complicates an investigation into host specificity of larval Digenea. However, where the species can be separated on morphological grounds, evidence of host specificity by the Digenea can often provide further evidence of phylogenetic relationships within the mollusc hosts.

In littoral Prosobranchs, James (1968) records the presence of seven cercarial types in one host species; four cercariae in two hosts; (invariably close species relatives e.g. gibbulids, patellids or littorinids), and finally three trematode species in three separate littorinid hosts. Thus, specificity of host selection does occur in shore gastropods, and James goes on to point out, that even when more than one host species is infected, a single host species is preferred.

Considering the parasitic fauna of British Littorina saxatilis, sub-species and varieties, James (1969) has drawn similar conclusions.

In fact, the study of the parasitic fauna of some animals can be the first evidence of sibling species. A pair of sibling species were discovered by Pickford and McConnaughey (1949) who examined the parasites of the Californian octopus. Some octopi were parasitised by one species of the mesozoan Dicyemennea, while other Octopus were infected by another species. Similarly, the turbellarian Polycelis nigra was divided in Britain into the two species P. nigra (MÜll) and P. tenuis (Ijima) by Reynoldson (1948), when he found that an average of 22 individuals of the petitrichian Urceolaria mitia occurred on P. tenuis, whereas only an average of 0.7 per individual were found on P. nigra.

In shore lamellibranchs, host specificity of the first larval digenean stage is probably as great as in littoral gastropods. Although Pelseneer (1906), records three cercarial types in nine, four and three separate bivalve hosts, this probably reflects the difficulty of separating different species of cercariae rather than a lack of host specificity. Bowers (1965) in a recent study of the larval digeneans of marine molluscs, records six species of first stage digeneans each infecting only a single species of lammellibranch. In a somewhat comparable study to the one reported here, Seed (1969) noted a higherincidence of the pea-crab Pinnotheres pisum in Mytilus edulis (L.) when compared with the 'Padstow mussel' (probably M. galloprovincialis Lamarck). Therefore, the variation in incidence of P. pisum in the two mussels supports the validity of separating the mussels into two morphological types. In the only comparative investigation available in the literature between the two Cerastoderma types, Fenchel (1965) found that in Baltic cockles two thigmotrichid ciliates Hypocomella raabei (= cardii) and Sphenophyra cardii occur in both C. lamarcki (= glaucum) and C. edule from the Øresund, Sweden, whereas two other ciliate species occur only in C. edule and three different ciliates only in C. lamarcki.

The two very closely related lamellibranchs of the genus Cerastoderma are considered to be separated at a variety or specific level. The symbiont fauna, including four larval Digenea of the two cockles has been studied to introduce further evidence for determining more exactly the systematic relationship between the two types and to assist in assessing the extent to which the forms have become biologically isolated.

Materials and Methods

Around the coasts of the British Isles can be found the two closely related cockles: Cerastoderma edule (L.) and Cerastoderma glaucum (Poiret). The suppresion of the genus name Cardium with reference to these cockles is considered elsewhere; see Section I.

The diagnostic, shell morphological characteristics of these two cockles have been formulated by Höpner-Petersen (1958) and perpetuated by Turk (1964), Tebble (1966) and Russell (1969). They have been separated using the following characteristics:-

Character		C. glaucum	C. edule
Shell shape	:	Elongated posteriorly	Almost oval
Ligament length	:	Short, confined to beneath umbo	Long
Ribbing	:	Sharply pointed triangular in cross-section; undeveloped on posterior region of shell	Flattened, present on posterior region of shell
Posterior Valve Junction	:	Almost straight	Crenulate
Periostracum	:	Well developed	Poorly developed

By the combined use of the above shell characters, separation into two cockle types can be achieved. To these can be added the internal anatomical feature of digestive gland colour and form. In C. glaucum the

gland is large, black and the secretory lobes are prominent and globular in appearance. In contrast the gland in C. edule is usually smaller in volume, the colour is more variable from dark green to pale brown, and the secretory lobes are usually less globular and distinctive, (Boyden, 1969).

Ecologically the cockles are also generally separable, as C. edule is predominantly a littoral dweller, whereas C. glaucum typically occurs in stagnant, marine, lagoons, (Boyden, 1969; Russell, 1969). However, an extensive mixed cockle population occurs in the River Crouch estuary, Essex. This population has permitted a comparative biological study to be undertaken where the environmental history of the two cockles is constant. The investigation recorded here forms part of a more extensive study to determine the biological separations between the two Cerastoderma.

A total of 2,401 C. edule and 2,969 C. glaucum were collected at regular intervals during the survey periods, May 1968 - September 1969, from the Crouch estuary at Hullbridge 'Ferry', Essex. The cockles were gathered from a single tidal level, between extreme low water springs and low water neaps, where both types commonly occur. Cockles between 2 and 6 years old with 2 to 6 annual rings were studied throughout.

To support the results obtained of the symbiont fauna of the Crouch cockles, a small sample of 91 C. edule and 23 C. glaucum was collected on the 10th October 1968, from a comparable mixed Cerastoderma population in the River Roach, Essex.

A survey of the symbionts found in homogeneous, single cockle populations was also conducted, to substantiate the normality of infection incidences found in Crouch cockles and to determine the effect of host ecology upon symbiont infection - see table 1.

Cerastoderma Type

C. edule			C. glaucum		
Location of Shore Sample	Date of Collection	Sample Number	Lagoon Location	Date of Collection	Sample Number
Tollesbury, Essex	19.10.69	32	New England Creek, Essex	26. 1.69	109
*Maplin Sands, Essex (S.L.A.S.)	11. 7.69	87	Sheerness Boating Lake, Isle of	17. 6.69	72
Southend, Essex	26. 1.69	104	Sheppy, Kent	25. 7.69	11
" "	27. 2.69	124	Widewater, Sussex	21. 4.69	8
" "	18. 5.69	71	" "	21. 7.69	21
" "	28. 6.69	29	Gosport Lagoon, Hampshire	7. 6.69	30
" "	31. 5.70	500	The Fleet, Dorset	12. 8.68	108
Whitstable, Kent	11.12.68	61			
Portsmouth, Horsey Island, Hants.	27. 5.69	34			
Poole Sandbanks, Dorset	21. 5.70	8			
Portland, Dorset	12. 8.68	31			
Malcolme, Devon	25. 3.69	17			
Wexford Harbour, Eire	13. 8.69	18			

Table 1. Date of collection and sample number of single cockle populations examined for symbiont fauna.

---

* My thanks to Mr. G. Pickett of Burnham-Shellfish-Laboratory who kindly obtained this cockle sample ~~of cockle~~.

All cockles were examined usually the same day, or the day following collection, being maintained during this period in air at 10°C.

Samples of mantle cavity fluid were removed by wide-mouthed pipette, and examined for symbionts using a monocular microscope. A gill lamella was removed and squashed beneath a cover slip. Tissue smears of the visceral mass were examined for trematode infection. The intestine was removed and squashed to determine infection by the Rhabdocoel Paravortex cardii. A special examination was made of the host tissue beneath the ligament and hinge line of all Cerastoderma, for the metacercarial stage of the gymnophallid parasite Meiogymnophallus minutus. The dissecting apparatus, slides and pipettes were cleaned between each cockle examination.

Sizes of symbionts were determined using a graduated micrometer eye and are expressed in mms.

Results and Observations

I. Incidence of Larval Digenetic Trematodes

The first three larval Digenea discussed below invade the visceral mass of the cockle attacking the gonad, digestive gland and haemocoel. The infection often spreads into the hoemocoelic spaces of the gill lamellae. Recent infections apart, the gonad is castrated. The fourth larval trematode occurs as metacercarial cysts beneath the ligament of C. edule which acts as second intermediate host.

These parasites have recently been described in detail by Bowers (1965) and thus morphological descriptions have in the most part been avoided in this work.

(1) Presence of Cercaria dichotoma (Lebour, 1911) non-Müller 1850

(= C. Fulbrighti, Hutton, 1952)

Super-Order - Anepitheliocystidia (La Rue)

Order - Strigeatodea (La Rue, 1926)

Super-family - Fellodistomatoidea (La Rue, 1957)

family - Gymnophalloidea

Description (see Plate 1)

Cercaria furcocerous. Young sporocyst stages are very active containing only germinal sacs. Large mature sporocysts (0.6 x 0.3 mm) are extremely numerous, irregularly ovoid, with a pronounced pointed end or spout, the 'birth pore' (Bowers, 1965). They contain many fully developed fork-tailed cercariae, each about 0.4 x 0.1 mm in size, including tail. A black, lyre-shaped excretory vesicle is clearly visible in the posterior portion of the cercarial body.

The metacercarial stage of this parasite has been located by Bowers (1965) in the polychaetes Nereis diversicola and Nephthys caeca. The adult gymnophallid worm is thought probably to occur in a shore duck.

Previous host records for this parasite are listed below:

Huet (1888) - In C. edule (L.) from the Normany coast.
(Cheng (1967) regards this gymnophallid as different from C. dichotoma calling it C. hueti sp. inc.)

Johnstone (1904) - In C. edule from the Lancashire coast.

Pelseneer (1906) - Present in C. edule and Macoma balthica (L.) from Boulogne-sur-Mer.

Lebour (1908) - In 25 of 50 C. edule examined from Northumberland coast occurred in Tellina tenuis (da Costa) from Fenham Flats, Northumberland.

Plate 1a) - Photograph of mother sporocyst of *Cercaria dichotoma* containing numerous cercariae.

0·25mm.

Plate 1b) - Cercariae of *Cercaria dichotoma* released from above sporocyst.

0·13 mm.

Plate 1a) -

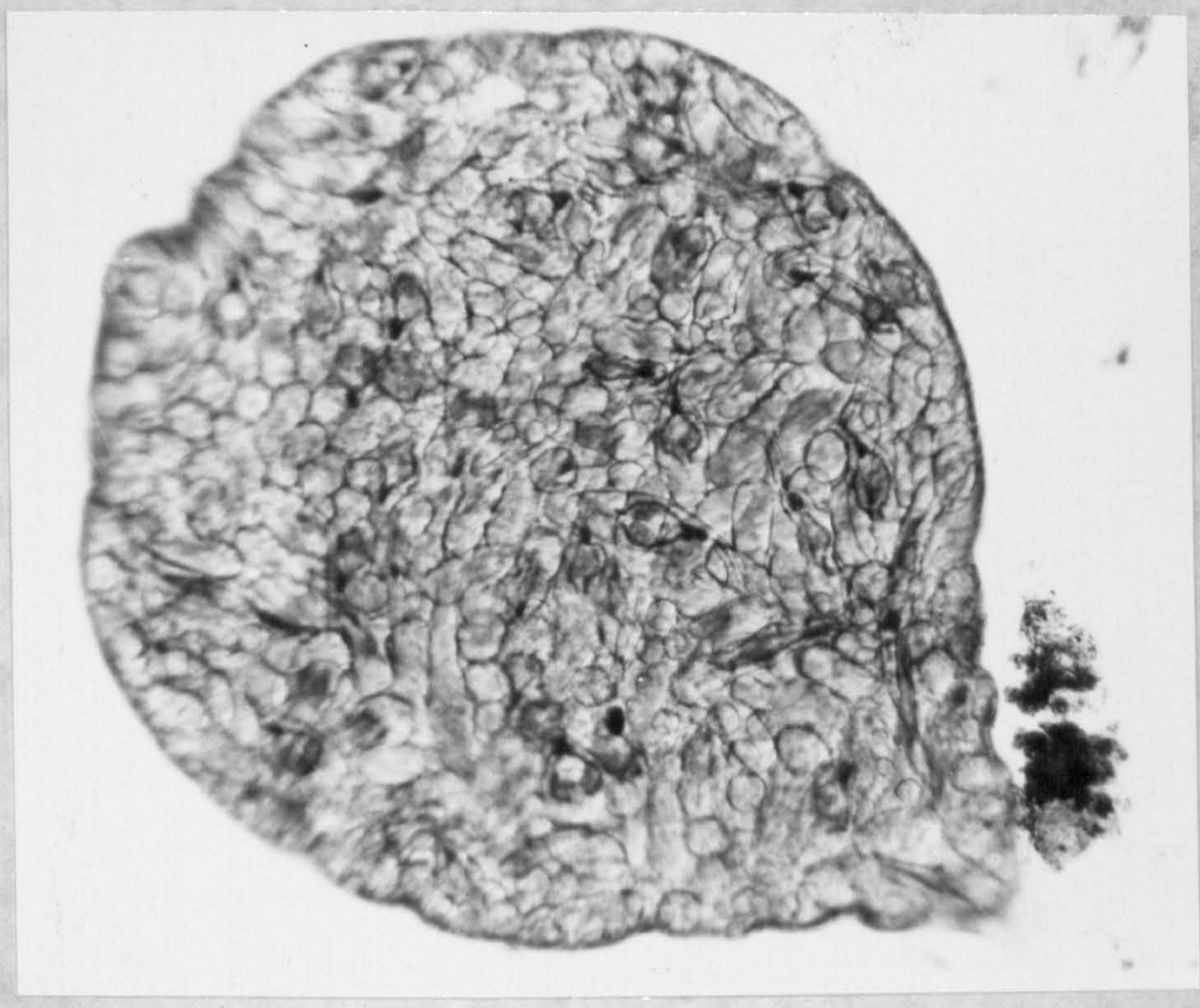
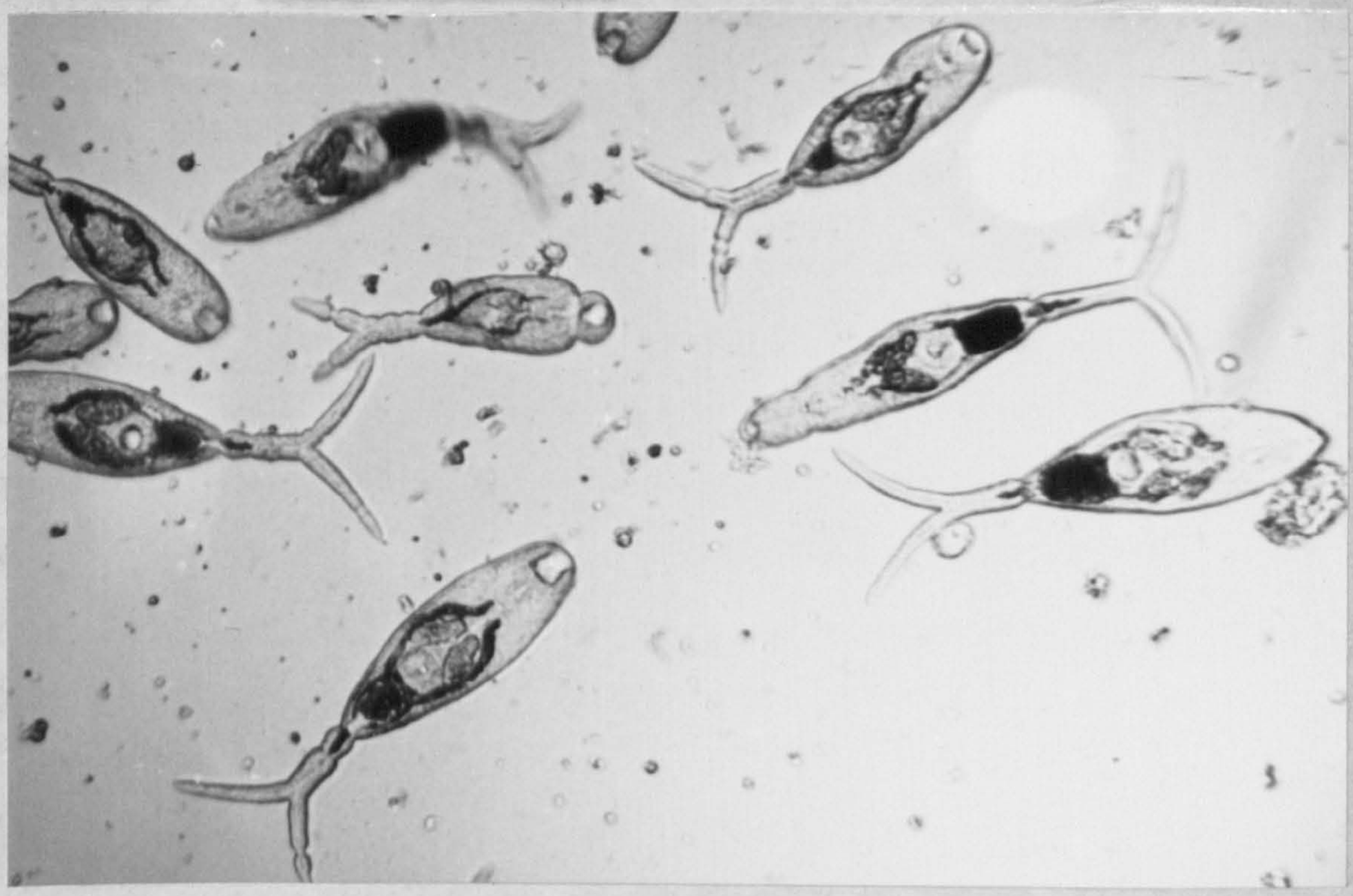


Plate 1b) -



Miller (1926) - In C. edule and T. tenuis

Hutton (1952) - 1.2% of 420 C. edule from Plymouth, Devon (as C. fulbrighti)

Cole (1956) - Records this parasite at Conway, N. Wales in C. edule

Bowers (1965) - 0.4% of 503 C. edule collected from Swansea Bay, S. wales. 0.3% of 10,500 C. edule from Llanrhidian Sands, S. Wales. 0.3% of 359 C. edule from Milford Haven, Pembroke.

White (1970) - In 0.23% of 2,610 Scrobicularia plana (da Costa) examined from South-East England.

The three gymnophallids of Cheng (1967), Cercaria hueti, C. dichotoma and C. fulbrighti are regarded here as synonymous.

Thus in the literature the incidence of infection of bivalves by this parasite is always low. Predominantly Cercaria dichotoma occurs in C. edule, although it has been found in the tellinids: Macoma balthica, Tellina tenuis and Scrobicularia plana which are also common, particularly shore bivalves.

Incidence of infection in the populations of Cerastoderma examined.

In cockles from the Crouch mixed population both C. edule and C. glaucum were infected. The incidence was 0.74% of 2,696 C. edule and 0.25% of 2,401 C. glaucum examined. Elsewhere two infected individuals were found in a sample of 18 C. edule collected from Wexford Harbour, Eire, and two parasitised individuals occurred in a sample of 89 C. edule from the River Roach estuary. One infected specimen was found in 54 C. edule examined from Whitstable, Kent.

No infected individuals were found during 1968-69 in 458 C. edule collected from the shore at Tollesbury and Southend, Essex and Portsmouth, Hampshire. However, one infected specimen occurred in 500 C. edule collected on the 30th May 1970 from Chalkwell, Southend, an incidence of 0.2%. Bowers (1968) records this trematode as absent from 48 C. edule examined from Lymington, Hampshire. No parasitised cockles were found in 250 C. glaucum collected from various saline, lagoon populations investigated around south-east England. This parasite appeared to be absent from The Fleet, Dorset; Gosport, Hampshire; Pidewater, Sussex; and Sheerness, Kent. However, a further 109 C. glaucum fron New England Creek lagoon, Essex, yielded two infected individuals.

Thus, C. glaucum as well as C. edule can be infected by this digenean. However, in the Crouch population the incidence of this parasite is somewhat less in C. glaucum than in C. edule. Lagoon populations of C. glaucum usually appear to be uninfected. However, the parasite has been discovered in one lagoon, New England Creek. This marine pool differs from other lagoons examined in that it is almost completely free from human interference. Thus, the presence of this parasite is thought to be due to the fact that the definitive host, considered to be a duck, visits this water.

In table 2 can be found the incidence of three developmental stages of Cercaria dichotoma in various Cerastoderma populations.

From table 2, it can be seen that the youngest sprocyst stages of this larval digenean were recognised from October until March, whilst the final cercarial stages were most common between May and August. It would seem that the duck definitive host is a winter migrant to the British coasts, occurring most commonly on the Essex coasts but also elsewhere, e.g. Llanrhidian Sands, Bowers (1965) and Wexford Harbour, South-East Eire.

Table 2. Incidence of three developmental stages of Cercaria dichotoma in various Cerastoderma populations

1. Very young sporocysts (containing germ balls only)	2. Sprocysts containing some cercaria	3. Heavy infestation of sprocysts each packed with mature cercariae
		30. 5.68 (C)
	13. 6.68	13. 6.68 (C)
	20. 6.68 (C) & 26. 6.68 (C)	20. 6.68 (C) & 26. 6.68 (C)
		11. 7.68 (C)
		7. 8.68 (C)
		11. 9.68 (C)
10.10.68 (R)	10.10.68 (R)	
		24.10.68 (C)
21.11.68 (C)		
11.12.68 (W)		
22. 1.69 (C)	22. 1.69 (C)	22. 1.69 (C)
26. 1.69 (N.E.C.)		
8. 3.69 (C)		
	22. 4.69 (C)	
	31. 5.70 (C)	
	15. 6.69 (C)	
	13. 8.69 (Wex.)	13. 8.69 (Wex.)

C - Infected Cerastoderma from Crouch mixed cockle population
R - Infected Cerastoderma from Roach mixed cockle population
S - Infected C. edule from Southend, Essex
Wex. - Infected C. edule from Wexford, Eire

2. Cercaria of Lepidopedon rachion (Cobbold, 1858), Stafford (1904)

Super-order - Epitheliocystida (La Rue, 1957)

order - Plagiorchiidae (La Rue, 1957)

Super-family - Allocreadioidea (Nicholl, 1934)

family - Allocreadiidae (Stossich, 1903)

Cobbold (1858) erected the name Distomum rachion for an adult digenean found in the intestine of various gadoid fishes (Dawes, 1946). The name Lepidopedon was substituted for Distomum by Stafford (1904), which has priority over Lepodora, used by Odhner (1905) and followed by Lebour (1908, 1911).

This larval digenetic trematode found in C. edule by Lebour (1905, and 1907) is suggested by Lebour (1911) to be the larval stage of Lepidopedon (= Lepodora) rachion.

Description

This monostome, leptocercous cercaria, develops in a broad chamber within sausage-shaped sporocysts (see plate 2). The cercariae have single tails, total size including tail, being (0.20 x 0.09 mm). The cercarial body is (0.160 x 0.08 mm) and is covered by transverse rows of minute spines. The youngest sporocysts contain germ balls within the broad chamber, which develop into cercariae and finally into metacercariae. Thus all the larval stages of this parasite occur within a broad chamber of a sporocyst. The small metacercariae are almost circular (0.22 x 0.15mm) and the tegument is covered by transverse rows of spines. From 5-15 metacercariae encyst within each sporocyst.

The colourless or grey sporocysts (0.60 x 0.15 mm) are usually very abundant in infected cockles, riddling the entire haemocoel and causing

Plate 2a) - Young sporocyst of Cercaria lepidopedon showing the single tailed cercariae.

0.16mm.

Plate 2b) - Mature sporocyst of Cercaria lepidopedon within which can be seen cercariae and six encysted metacercariae. Note the prominent brood chamber containing the developmental stages.

0·2mm.

Plate 2a)

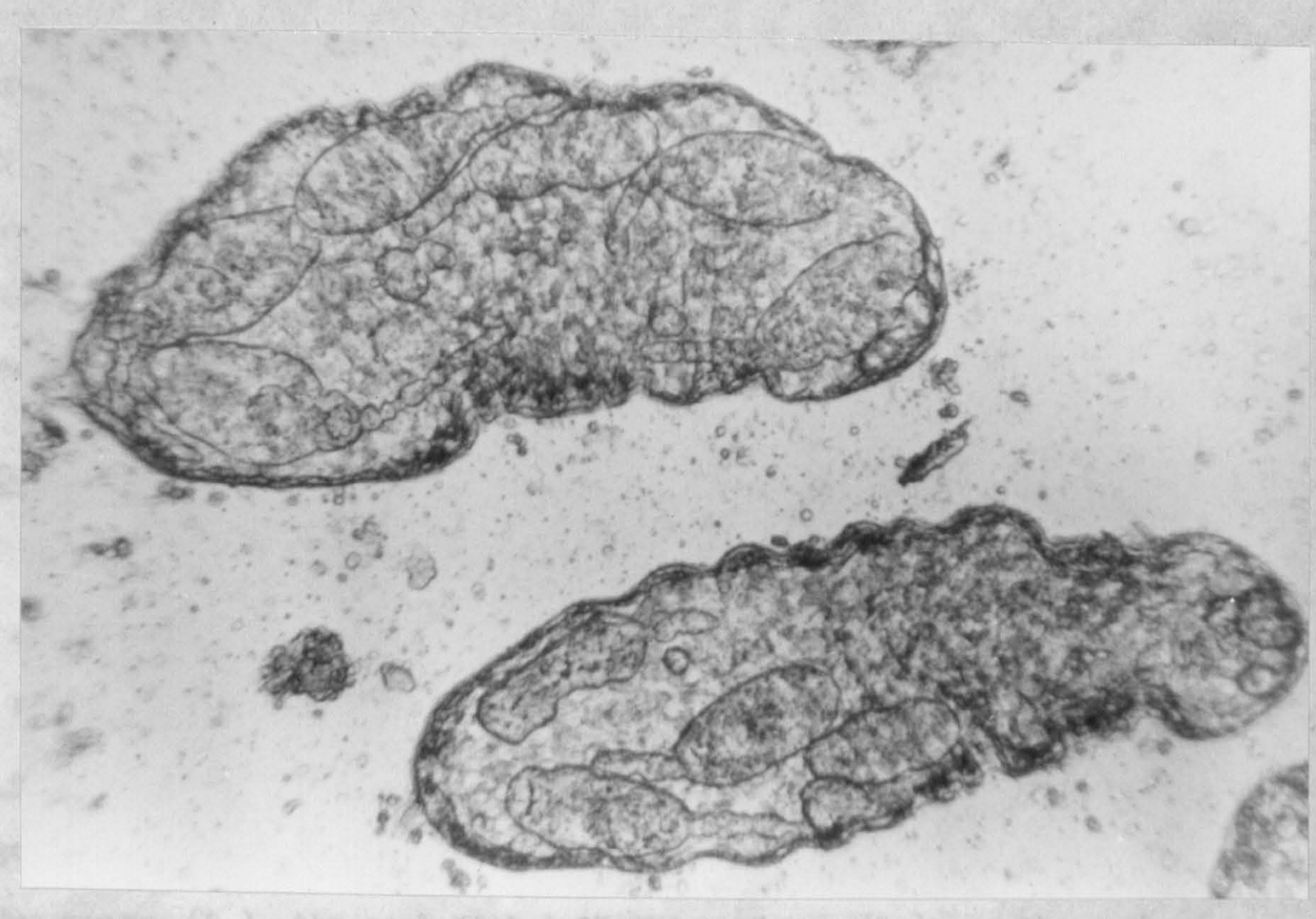
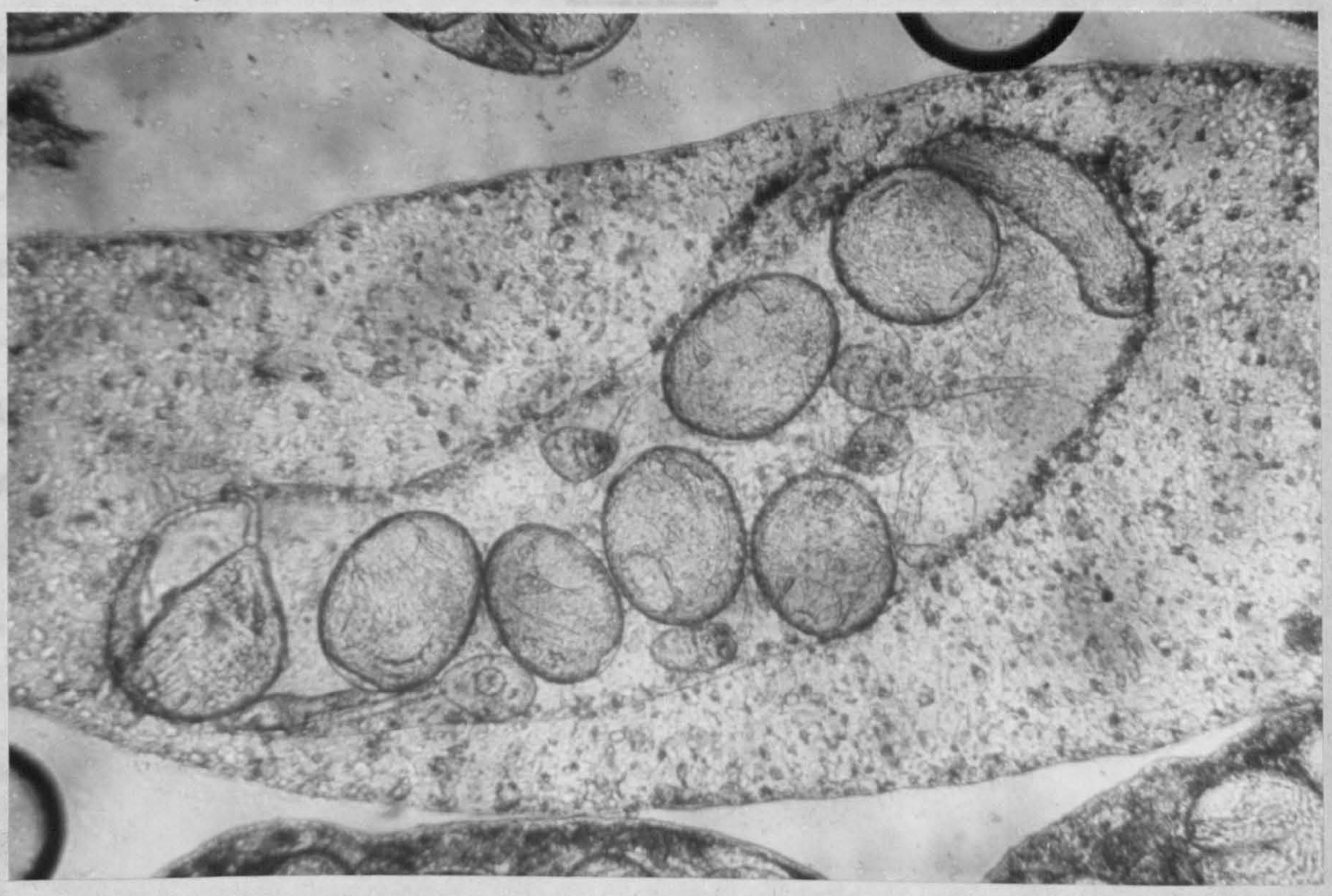


Plate 2b)



distencion of the viscera and gills. They are thick walled and active and the outer wall has a speckled appearance. Bowers (1965) noted the presence of two layers of muscle, and a sub-tegumental layer composed of mesenchymal and germinal cells. The broad chamber is suspended from the outer sporocyst wall by strands of connective tissue.

Life History

Since a major food of the haddock Melanogramus aeglefinus (L.) is cockles, (Lebour, 1908), and because the trematode L. rachion found in the intestine of the haddock was similar to the metacercariae found in C. edule, Lebour (1911) suggested the synonomy of these larval and adult digeneans, Dawes (1946) records L. rachion in M. aeglefinus, the cod Gadus morhua (L.), the coal-fish Pollachius virens (L.) and the pollack P. pollachius (L.). To this list Sprehn (1933) adds the whiting Merlangius merlangus (L.) and the hake Merluccius merluccius (L.).

Previous records of larval stages

- Johnstone (1904) recorded one C. edule infected with cercariae of L. rachion in a sample of 100 C. edule collected in October from Morecombe Bay, Lancashire.

- Lebour (1905) records on infected specimen out of 200 C. edule examined from Budle Bay, Northumberland.

- Lebour (1907) again records a single C. edule out of 100 individuals collected from Holy Island, Northumberland. Both the above infected cockles recorded by Lebour contained metacercarial cysts and were collected in March and April respectively.

- Lebour (1911) reviews the three infections above.

- Bowers (1965) noted 1 infected individual out of 200 C. edule examined from the Kyle of Tongue, North Scotland.

Thus, the larval stages of this parasite are rare and have only been previously recorded in four C. edule.

Incidence of L. rachion in the Cerastoderma examined in this investigation

Individuals of both Cerastoderma types from the Crouch mixed population were found to be infected. Thus this larval digenean occurred in three C. glaucum (0.12%) and two C. edule (0.07% incidence). One infected cockle was discovered in a sample of 41 C. glaucum collected from the River Roach estuary, Essex.

At Southend, Essex the C. edule population was found to be infected as follows:

Locality of Sample	Date of Sample	Nos. of C. edule examined	Nos. infected by L. rachion	% incidence of infection
Southend foreshore	Jan. 26.1.69	104	8	7.7
" "	Feb. 27.2.69	124	9	7.3
" "	May 18.5.69	71	1	1.4
" "	June 28.6.69	29	-	-
Maplin Sands	July 11.7.69	87	2	2.3
Total Incidence:		415	20	4.8 %

However, a further sample of 500 C. edule collected from Chalkwell, Southend on the 30th May 1970 yielded only one infected specimen: an incidence of 0.2%.

No other populations of Cerastoderma were found to be infected. This parasite was absent from 240 C. edule collected from Poxford Harbour, Eire; Salcombe, Devon; Portsmouth, Hampshire and Whitstable, Kent. 359 C. glaucum from the various lagoon populations examined around the south-east coasts of England were also uninfected.

The absence of this parasite from land locked lagoon populations of C. glaucum supports the contention that the definitive host is a marine fish.

This parasite has previously been regarded as extremely rare as only four infected C. edule have been recorded in the literature. Yet this investigation yielded 27 infected Cerastoderma. The definitive host was suspected by Lebour (1911) to be the haddock M. aeglefinus, but as noted above, from Daves (1946) and Saprehn (1933) a total of six Hake and gadoid fishes can be hosts of the adult L. rachion. Although the relationship between larval stages in the cockle and the adult worms is the intestine of gadoids has not yet been experimentally proved, this could well be another example of less specific host selection of the adult compared with the larval stage, as the suggested adult digenean is found in six separate fish species, whereas the probable larval stage only occurs in the cockles of the genus Cerastoderma.

It is interesting that normally the hake and gadoids listed above are northern cold water fishes but correlated with exceptionally successful spawning extensions of the normal range of the species can occur (Wheeler, 1969). Thus in the last few years the haddock and cod especially have extended southwards into the southern North Sea. Certainly the catches of haddock in the Thames Estuary have been unprecedented as recorded in the popular angling press; haddock having been caught up-river as far as Greenwich Power Station. It would therefore seem likely that the migration of the final host has primarily been responsible for the high incidence of infection discovered in the Essex littoral Cerastoderma populations during 1968-69.

Table 3. Presence of Young, Developing and Fully Developed Stages of Lepidopedon rachion in Cerastoderma Populations from South-East England

Age of majority of sporocysts infected cockles.

Young Sporocysts (Containing germ balls in the brood chamber)	Developing Sporocysts (containing mainly cercariae in the brood chamber)	Fully Developed Sporocysts (Containing mainly metacercariae)
		30.5.68 (C)
		6.6.68 (C)
		11.9.68 (C)
	10.10.68 (R)	
	26. 1.69 (S)	26.1.69 (S)
27.2.69 (S)	27.2.69 (S)	27.2.69 (S)
18.5.69 (C)		18.5.69 (S)
		31.5.70 (S)
		10.7.69 (S)

(C) - Infected Cerastoderma from Crouch mixed population, Essex

(R) - Infected Cerastoderma from Roach mixed population, Essex

(S) - Infected C. edule from Southend, Essex

It can be seen from table 3 that the youngest stages of this cercaria are found mainly during late winter and spring whilst the later developmental stages seem to occur throughout the year. The time of infection is probably regulated by the appearence of the definitive host,

probably a gadoid over the cockle beds during the winter months.

Thus, although the parasite is extremely specific in selection of the genus Cerastoderma as larval host, it appears equally able to infect C. edule and C. glaucum.

3. Cercaria Bucephalopsis haimeana (Lacaze-Duthiers, 1854)

Super-order - Anepithcliacystidia (La Rue, 1957)

order - Strigeatoidea (La Rue, 1926)

Super-family - Bucephaloidea (La Rue, 1926)

family - Bucephalidae (Poche, 1907)

Description

The long, thin, tubular sporocysts, coloured either orange or cream, form a tangled irregularly branched mass within the viscera of the cockle. All stages of development, from germ balls, through young cercariae with short tails, to fully tailed cercariae, occur within the sporocyst (see plate 3). Reproduction within the daughter sporocysts has been thoroughly described by James and Bowers (1967).

The fork-tailed cercariae have long, contractile furca, attached to the body by a tail stem. The body size is 0.26 x 0.05 mm, while the tails may be many times longer than the body. The body has a striated appearance, bearing transverse rows of minute cuticular spines. Posteriorly there is a pale, pear-shaped excretory vesicle.

Life Cycle

The complete life cycle has been postulated by Lebour (1911). The encysted metacercariae of a bucephalid were first discovered by Haddox (1867) in the nerves of the haddock Melanogrammus aeglefinus. Johnstone (1904)

Plate 3a) - Developmental stages of the cercariae of Cercaria Eucephalopsis haimeana.

0·12 mm.

Plate 3b) - Fully developed cercaria and section of the tubular sporocyst of Cercaria E. haimeana.

0·12 mm.

Plate 3a)

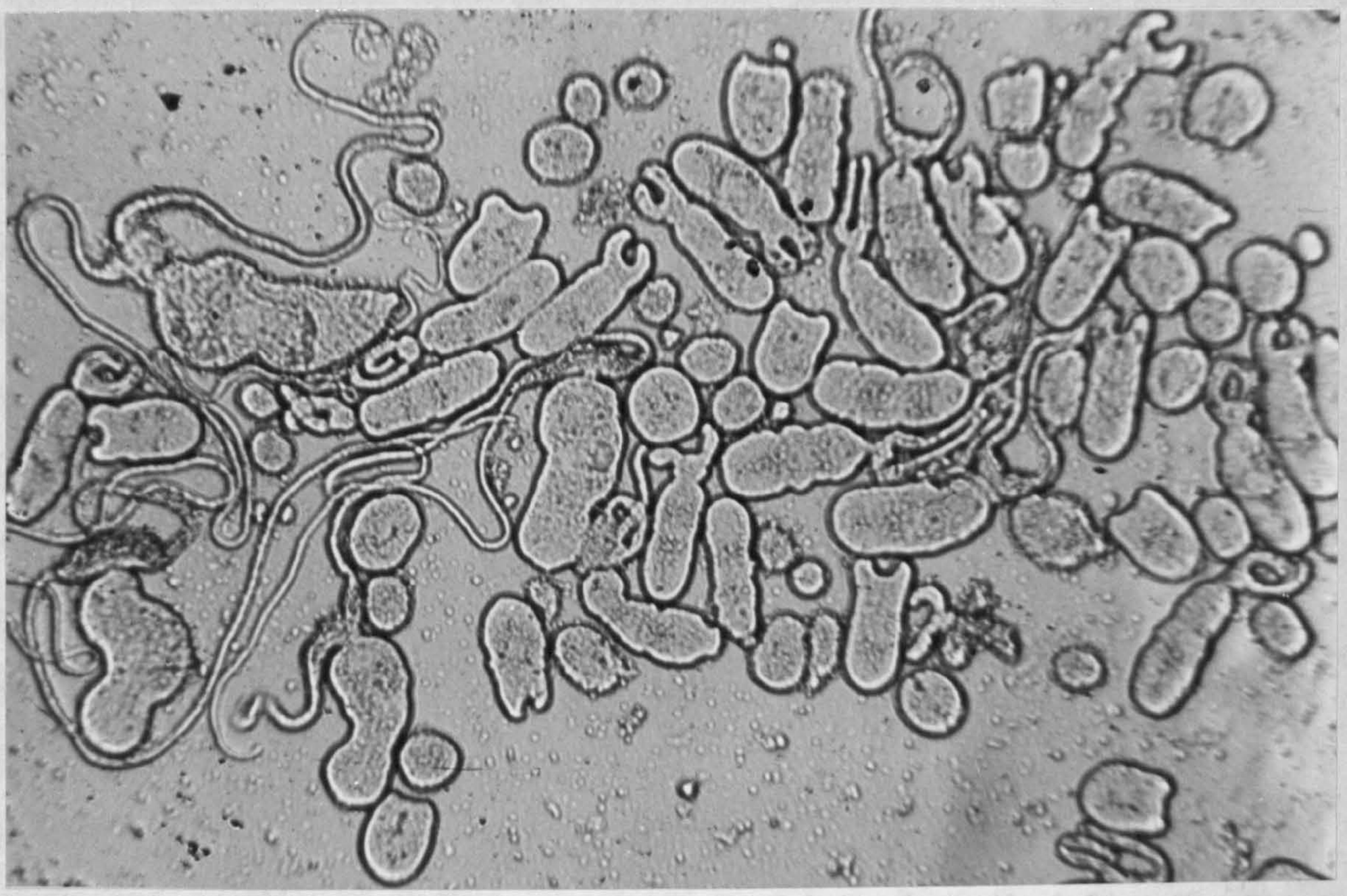
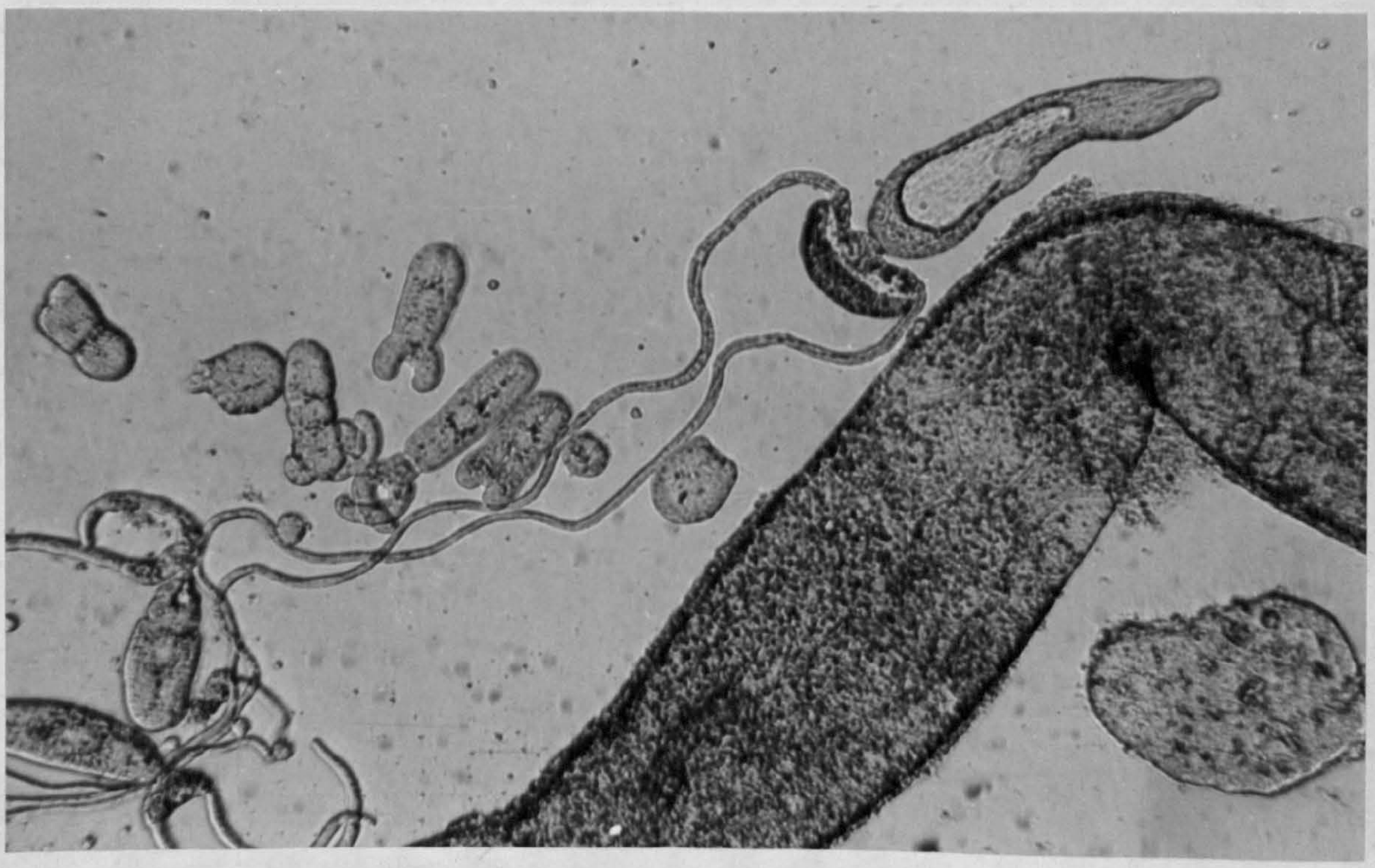


Plate 3b)



records metacercarial cysts of a bucephalid in gadoid fish, and in Phycis blennioides. Williamson (1911) also found such cysts in the skin of various gadoids. Lebour (1911) located encysted metacercaria in the nerves of gadoids especially the haddock Melanogramus aeglefinus (L.), the cod Gadus morhua (L) and the whiting Merlangius merlangus (L.). Because of the similarity of these metacercariae to the adult bucephalid Gasterostomum gracilescens which is found in the stomach and pyloric caeca of the angler fish Lophius piscatorius (L.) and the conger eel, Conger conger (L), Lebour hypothesized the life cycle as: first larval stages in C. edule; metacercarial stage encysted in gadoids; and finally definitive host as L. piscatorius and C. conger. However, this is by no means a proven life cycle, because as pointed out by Cheng (1967), at least 145 species of adult bucephalids have been described from fishes, (Yamaguti, 1958), but only a few larval bucephalids have been recorded from molluscs.

Nicholl (1914) renamed the bucephalid parasite of C. edule as Bucephalopsis haimeanus because of differences between it and the type species of Bucephalus, B. polymorphus. ~~James et al~~ Bowers (1966) redesignated this larval digenean as Cercaria Bucephalopsis haimeana and this nomenclature has been followed here.

Previous records of first larval stages of Cercaria B. haimeana in lamellibranchs

Lacaze-Dulthiers (1854) - Discovered a bucephalid in Ostrea edulis (L.) and Acanthocardia tuberculata (L.) from the Mediterranean.

Moulinie (1856) - Also as above

Huet (1888) - In C. edule (L.) from the Normandy coast of France.

Johnstone (1904) - In C. edule from the Lancashire coast.

Pelseneer (1906) records B. haimeanus in the following lamellibranchs: C. edule; Abra Alba (Wood); Spisula Subtruncata (da Costa); S. solida (L.); V. pullastra (Montagu); Ostrea edulis and A. tuberculata; (from the Mediterranean) and Donax trunculus (L.). Lebour (1911) records an incidence of 2% in 100 C. edule examined from Fenham flats, Northumberland and 10% incidence at Ainsworth, Hampshire. She also records Bucephalus syndosmyae sp. inq. from Abra alba.

Johnstone (1921) - 5 out of 54 C. edule, 9.2% incidence on Lancashire Coast.

Cole (1938) - records Bucephalus mytili (for further details see Cheng (1967) p.209-211). This bucephalid is clearly a separate species to Cercaria B. haimeana.

Rees (1939) - C. edule from the Dovey Estuary, Wales

Hutton (1952) - Rarely in C. edule from Plymouth, Devon.

Cole (1956) - 2% incidence in C. edule from Conway, North Wales.

Figueiredo et al (1964) - 5.6%, 7 out of 125 C. edule examined from Ria de Aveiro, Portugal.

Hancock & Urquhart (1965) - Average of 8% incidence, 40 infected out of 468 C. edule from Llanrhidian Sands, South Wales.

Bowers (1965) - 1% of 503 C. edule from Swansea Bay, South Wales.

- 8% of 10,000 C. edule from Llanrhidan Sands, South Wales.

- 25% of 359 C. edule from Milford Haven, Pembroke, South Wales.

Incidence of Cercaria B. haimeana in the Cerastoderma

During this study of the Crouch mixed cockle population 318 infected C. edule were recorded from a total of 2,969 examined, an incidence of 11.8%; whereas only one infected C. glaucum occurred in 2,401 individuals of this cockle examined. The single parasited C. glaucum was castrated, the visceral mass being full of tangled, orange sporocysts. It is apparent therefore that a much higher incidence of infection was recorded in C. edule compared with C. glaucum. From the Roach mixed population, no C. glaucum (23 examined) were infected but the incidence in C. edule was 6.7% of 89 examined.

Elsewhere single cockle populations of C. edule, from littoral locations were invariably parasitised, see below:

Locality	Nos. of cockles examined	Nos. of individuals parasitised by Cercaria B. haimeana	% incidence of infection
Wexford Harbour, Eire	18	1	5.6%
Salcombe, Devon	17	-	-
Portland, Weymouth, Dorset	31	-	-
Poole Harbour, Dorset	8	1	(12.5%)
Portsmouth, Horsey Island foreshore, Hampshire	34	13	38.2%
Whitstable, Kent	61	3	4.9%
Southend, Essex, 1968-69	415	7	1.9%
Tolesbury, Essex	32	3	9.4%
Southend, Essex, May 1970	500	4	0.8%

Parasitised C. glaucum were absent from totally land-locked lagoons. Thus no infection was found in 251 individuals from New England Creek, Widewater, Sheerness, or Gosport marine pools. Neither was there any infection in 75 C. glaucum from permanently submerged locations of the Fleet, Dorset. However, in 33 C. glaucum individuals collected from the lower reaches of the Fleet, four infected specimens were discovered. These cockles were shown to be C. glaucum by their shell morphological characteristics and their black digestive glands. These cockles were, however, extremely stunted, being at the maximum 25 mm long, more usually 15 mm long. They were also exposed to the air for several hours during low tide, this being in direct contrast to the remainder of the population of this cockle found elsewhere in the Fleet. In comparison with these C. glaucum from permanently submerged regions the stunted cockles appeared to be in poor condition. This sample was collected adjacent to a small jetty used by fisherman ferrying across the Fleet to Chesil beach. In the immediate vicinity of this jetty were intestines and head remains of numerous fish, gutted by the fishermen. It is suggested that this infection of C. glaucum was due to a nucleus of infection, originating from adult Bucephalus (= Gasterostomum) in the gut remains of conger eels. The physiologically poor condition of these cockles; reflected in their stunted condition may well have made them more susceptible to infection. The anomalous nature of this infection is further supported by the fact that neither C. glaucum from permanently submerged localities of the Fleet or C. edule from littoral locations (of however higher salinity) at the Fleet mouth were infected by Cercaria B. haimeanus.

Bowers (1965) studying the incidence of infection of this parasite in C. edule or Milford Haven, Pembroke, found that it varied along the estuary, decreasing with increase in salinity. The work recorded here

generally supports this observation; low or no infections were found in C. edule for the most saline locations, at Lexford Harbour, Salcombe and Portland. At Whitstable and Southend, where the salinity is reasonably high, about 32-34‰ but generally lower than the aforementioned sites, the incidence of infection averages 4.2%. This is much lower than the average 12.1% found in the upper Crouch estuary where the salinity is very variable and generally low: from 8.5-31.5‰: It may of course be shown that the definitive host is more common in estuaries than in open shore locations which could also cause the above incidence pattern.

It is interesting to note that Hopkins (1954) concludes that B. haimeanus only occurs in its most common host/Ostrea edulis in areas which are bathed by saline oceanic waters; in comparison with the American species B. cuculus which occurs in Crassostrea virginica found in more land-locked, estuarine waters of lower salinity. The bucephalid found in C. edule is also more abundant in areas where salinity is generally fairly low and variable. Since metacercarial cysts of bucephalids have been recorded from different tissues in various hosts, and as so many different adult bucephalids have been described, the evidence above may suggest that although morphologically very similar, the larval stages recorded in Ostrea edulis (Hopkins, above), Acanthocardia tuberculata, Abra Alba (see earlier) and C. edule may not be of a homozygous genetic stock.

The high incidence of infection 38.2% in the Portsmouth cockles examined is in direct contrast to a total absence of infection recorded by Bowers (1965) in 48 C. edule collected from Lymington, Hampshire.

• Salinities at Brandy Hole, River Crouch, 1966-67, from Burnham Shellfish laboratory, Burnham-on-Crouch, Essex.

TABLE 4 - Incidences of total infection (and light infections) of C.edule from the Crouch estuary by Cercaria Bucephalopsis haimeana

	Month of Collection	No.of C.edule examined	No.of bucephalid parasitised cockles	Percentage Incidence	No.of cockles with light infestation of bucephalid	Percentage incidence
1968	May	254	33	13.0	5	1.97
	June	360	37	10.3	3	0.83
	July	183	20	10.9	2	1.11
	August	190	36	18.9	11	5.8
	September	194	30	15.5	11	5.7
	October	142	16	11.3	10	7.0
	November	208	18	8.7	7	3.4
	December	184	26	14.1	4	2.2
1969	January	212	26	12.3	7	3.3
	February	-	-	-	-	-
	March	130	18	13.8	6	4.6
	April	191	17	8.9	3	1.5
	May	203	14	6.8	6	2.9
	June	126	10	7.9	3	2.3
	July	74	10	13.5	1	1.3
	August*	42	5	14.3	1	2.4
	September*	15	2	13.3		

(* - low sample numbers)

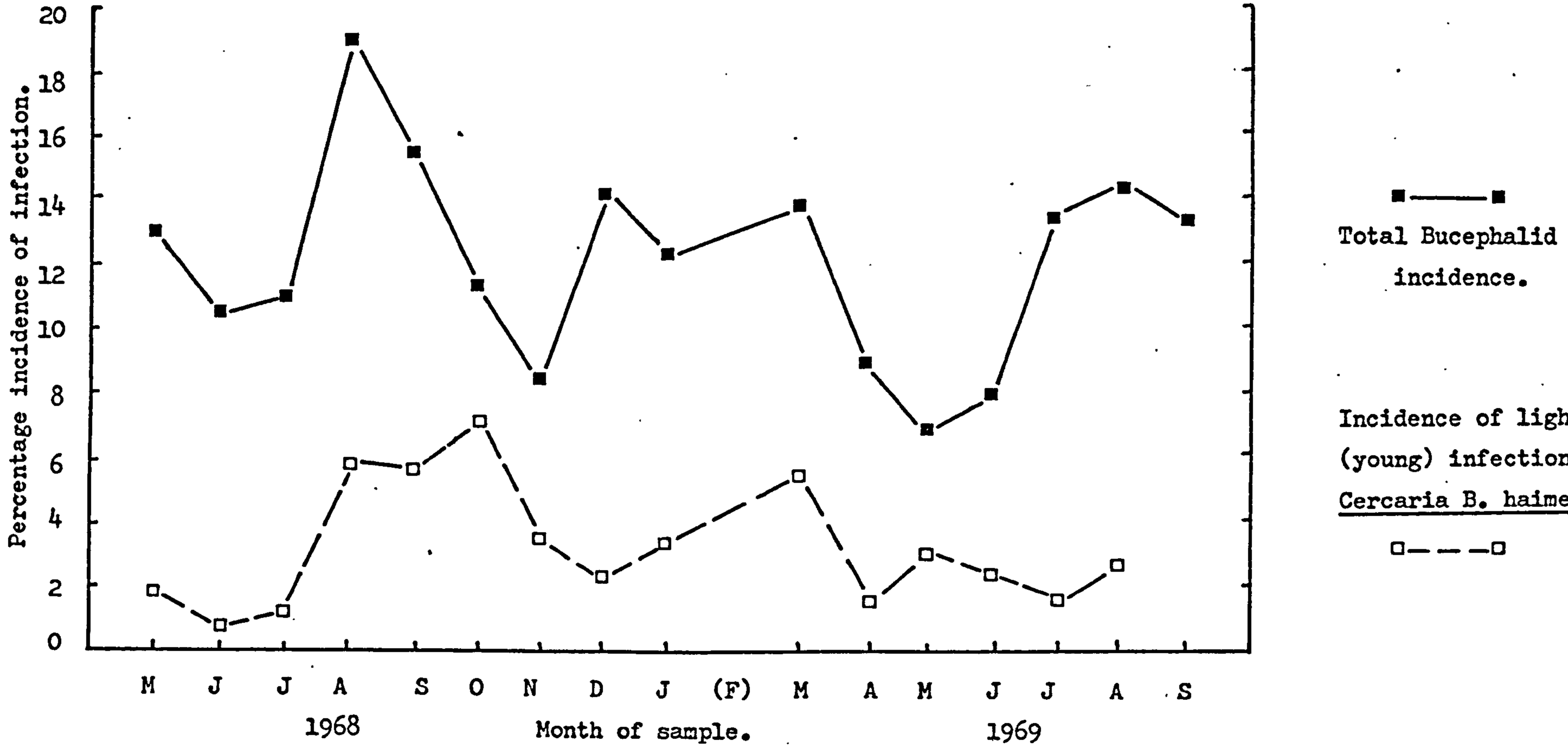


Fig 1 - Variation in the incidence of infection of C.edule from the Crouch estuary by Cercaria B. haimeana between May 1968 and September 1969.

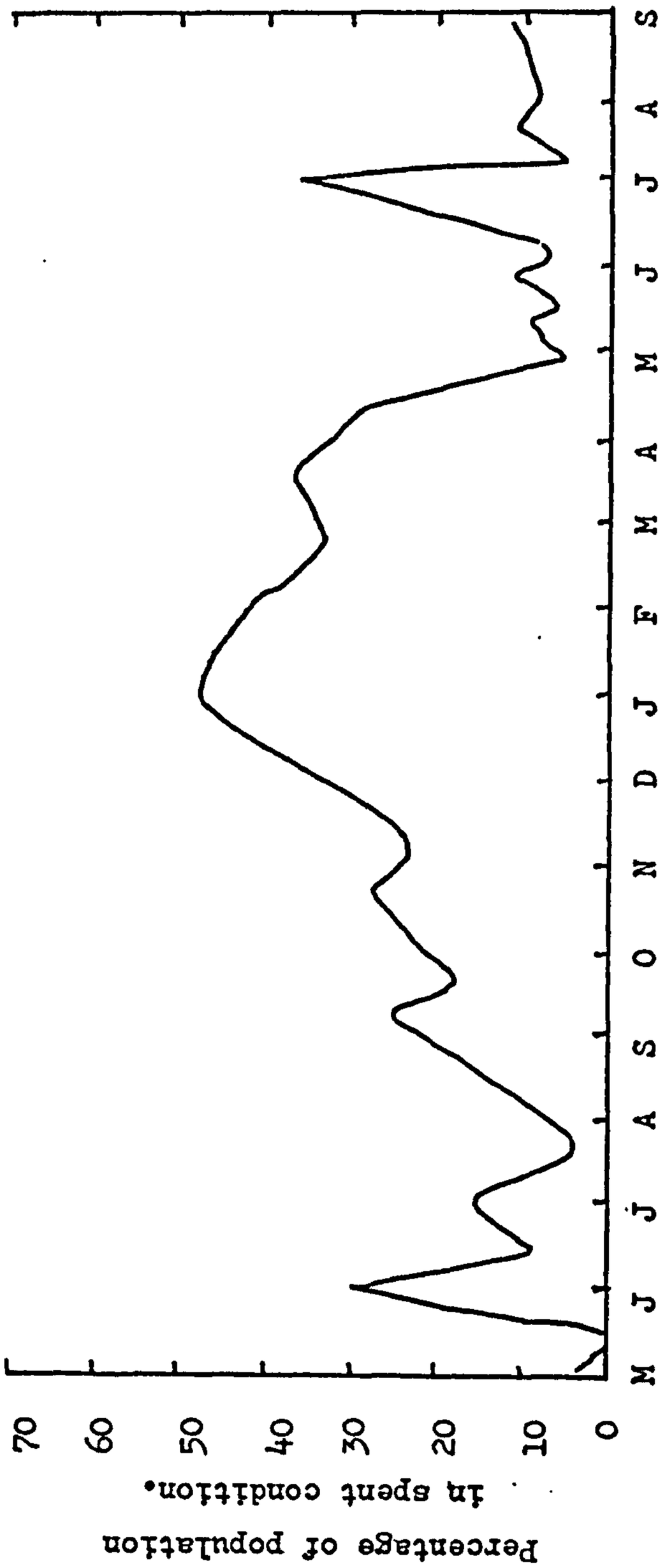


Fig 2 - Percentage incidence of spent C.edule in the Crouch population from May 1968 until September 1969.

This great variability of infection incidence is probably related to local factors affecting the abundance of the definitive host, rather than environmental characteristics, e.g. salinity, affecting the first infective stage of this parasite.

The seasonal variation in the percentage of C. edule from the Crouch estuary by Cercaria B. haimeana (see table 4) is graphed in figure 1. Bowers (1969) records a sharp increase in percentage infection of Cercaria B. haimeana in C. edule between May and August. A similar phenomena is shown in figure 1 where two major peaks of infection can be seen in August 1968 and 1969. Bowers by comparing the breeding cycle of C. edule with the percentage infection of this cercaria, concludes that only spent cockles become infected by this parasite. The percentage of spent individuals of the host, is plotted on figure 2. It can be seen that during the spawning seasons the spent individuals of the cockle population reach a peak at the end of May - beginning of June, in July and finally in September. However, indeterminate individuals also occur at a higher percentage throughout the winter months. It would therefore seem likely that infection is associated with spawning.

During the summer of 1968, six individuals parasitised by Cercaria B. haimeana were noted each containing various quantities of developing ova. The relatively rare presence of infected cockles with gametes has been recorded previously by Hancock and Urquhart (1965) and Bowers (1965). It may not, therefore, be necessary for the potential host to be entirely spent before penetration by the infective bucephalid miracidium, but only that the host be weakened by the process of spawning or partial spawning.

The distribution of the youngest stages of this parasite is also plotted in figure 1. The percentage incidence is greatest during the

summer months from August to October, in the period when C. edule is undergoing spawning and thus recently spent individuals are found in the population. As the first peak of spent C. edule occurs at the beginning of June, and the first peak of light bucephalid infestation is found in August, it may be suggested that a period of two months is required for consolidation of the infection, between the infective miracidial stage and the recognisable light infestation of the cockle.

Thus, it is suggested that the normal host of Cercaria B. haimeanus is C. edule, but infection of C. glaucum can occur, although probably only in exceptional circumstances.

4. Metacercaria of Meiogymnophallus minutus (Cobbold, 1859)

Super-order - Anepitholiocystidia (La Rue, 1957)

order - Strigeatoidea (La Rue, 1926)

Super-family - Fellodistomatoidea (La Rue, 1957)

family - Gymnophallidae (Horozov, 1955)

Bowers and James (1967) demonstrated the synonymy of:

Distomum minutum (Cobbold, 1859)

Cercaria margaritae (Lebour, 1907)

Gymnophallus oedemiae (Jameson & Nicoll, 1913)

and Cercaria cambrensis (Cole, 1938)

Description

Beneath the umbo of C. edule are found encysted metacercariae varying in number from a few, in young cockles, to many hundreds in large, old individuals. The metacercariae are oval and minute (see plate 4) measuring 0.22 x 0.10 mm and the tegument is covered by

Plate 4a)

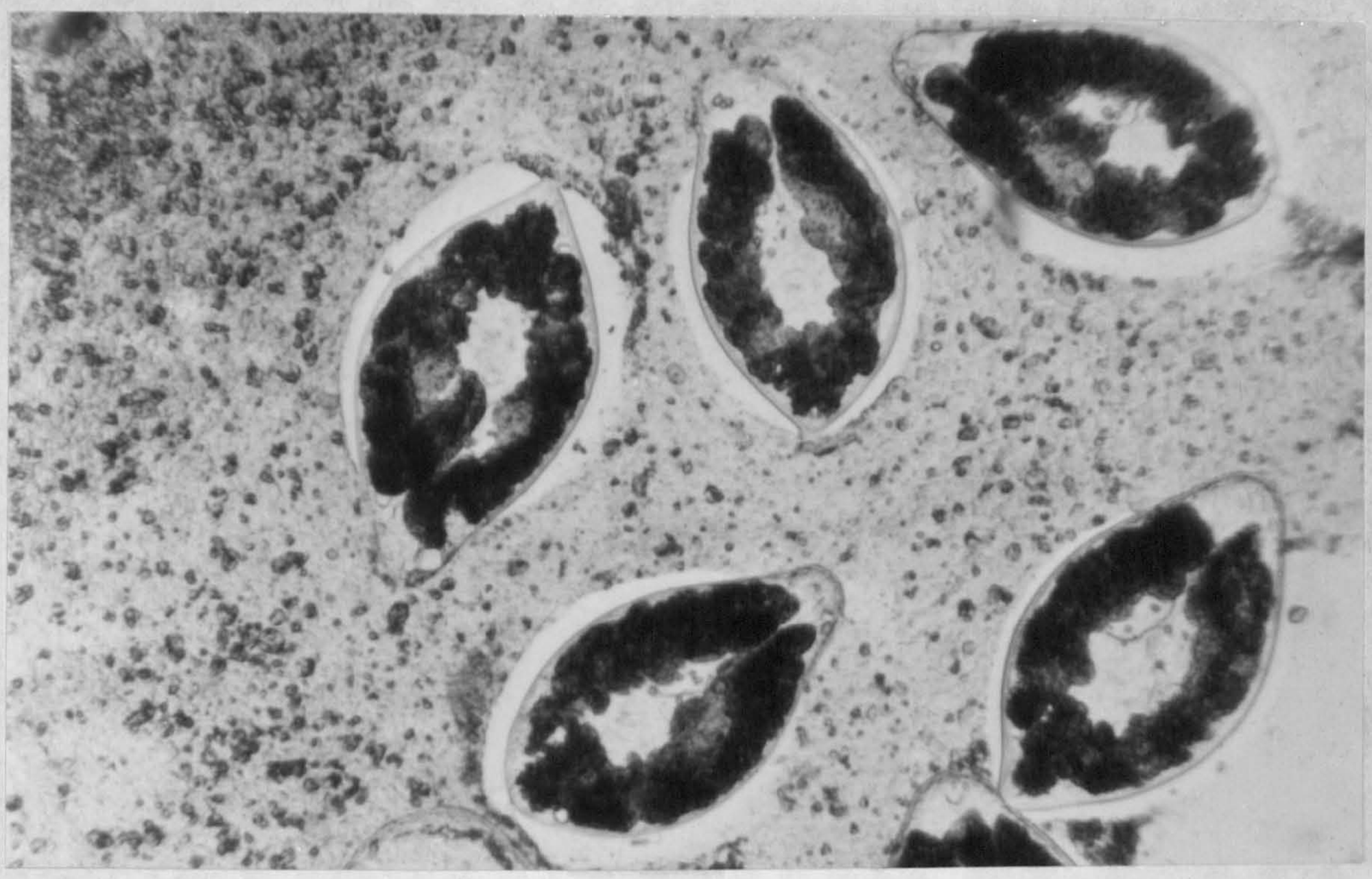
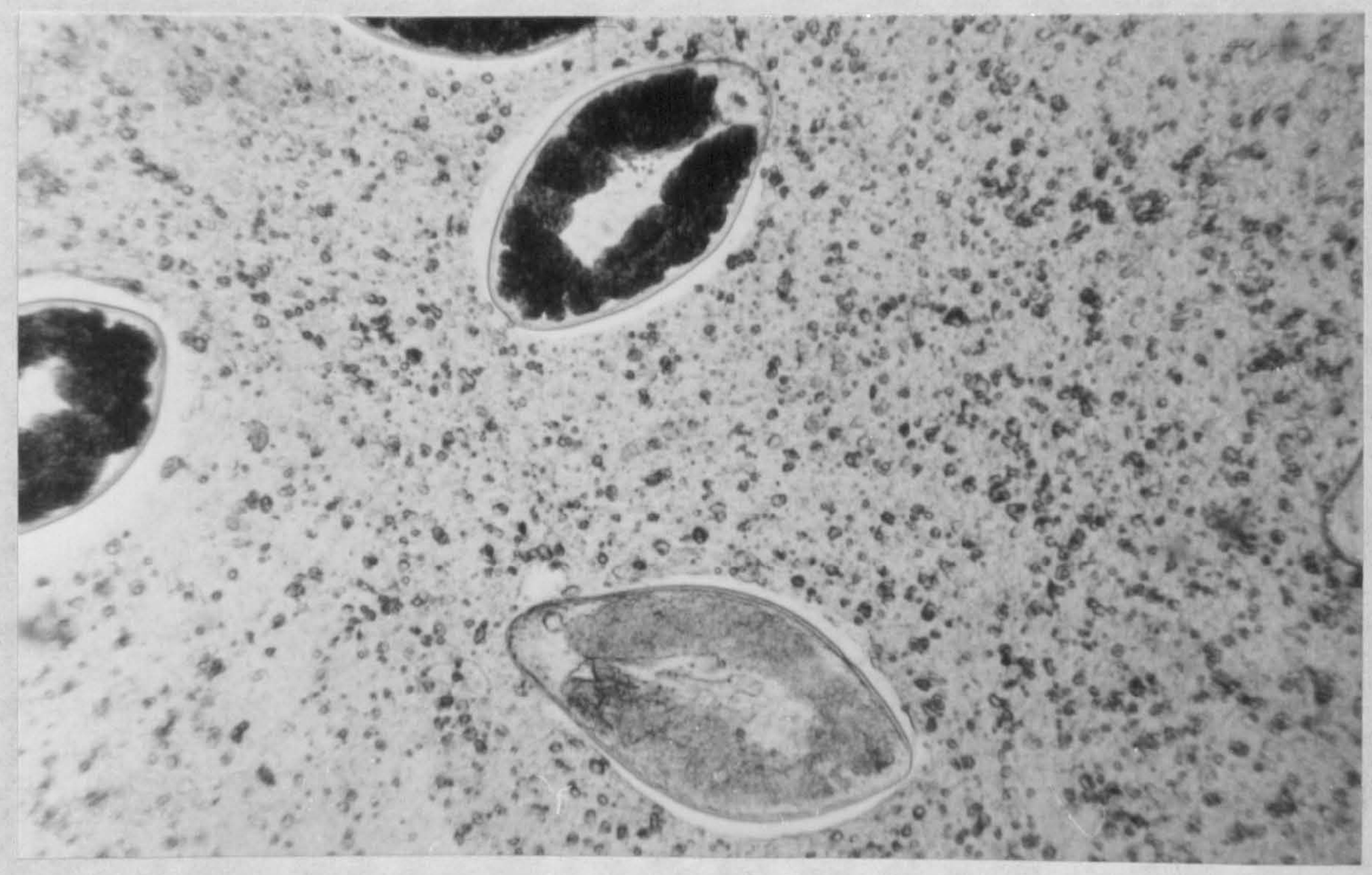


Plate 4b)



transverse rows of spines. A full description can be found in Bowers and James (1967). The Y-shaped excretory vesicle is very prominent reaching from the posterior excretory pore almost to the oval sucker. It is filled by dense, black coloured, excretory granules. The ventral sucker varies in size between 0.025 - 0.028 mm. and the anterior sucker from 0.037 - 0.039 mm.

These metacercariae are found in a very localised area, surrounded by host tissue in the region of the valve cardinal teeth. The host tissue in the region of the cysts is distinctly pale brown coloured. They occur beneath the ligament usually in tissue between the posterior cardinal tooth and the posterior lateral teeth. Some metacercariae especially in the River Roach C. edule are larger in size (0.28 x 0.15 mm.) and the body appears grey instead of black; (see plate 4). These individuals are thought to be equivalent to those recorded by Bowers and James (1967) as infected by the microsporidian protozoan Nosema sp.

Previous records of Lamellibranch hosts

There are several gymnophallid metacercariae which infect the mantle, or occur between the mantle and the shell valves of various bivalves. These have been summarised by Bowers (1965). Only those records of numerous gymnophallid metacercariae associated together in communial cysts are listed below:

Jameson (1902) records this trematode as sporocysts of Lecithodendrium somateriae in C. edule and Venerupis decussata from the Lancashire coast. The location of the cysts in the former host was beneath the umbo, in the latter they are recorded in the dorsal borders of the siphonal muscles.

Nicoll (1906) - as sporocysts containing cercariae under the hinge in C. edule, collected from the Eden Estuary, St. Andrews, Scotland.

Lebour (1907, 1911) - as Cercaria margaritae occurring in cysts beneath the hinge, in C. edule from the Northumberland coast.

Cole (1938) in C. edule from Conway, North Wales, 100% infection out of several thousand examined: (As C. cambrensis)

Rees (1939) in C. edule from the Dovey estuary, Wales.

Hutton (1952) in C. edule from Plymouth, Devon

Figueiredo et al (1964) - As C. cambrensis (Cole) in C. edule, 16% incidence from Ria de Aveiro, Portugal.

Bowers (1965) in C. edule - 84% of 503 individuals from Swansea Bay.

- 100% of 10,500 specimens from Llandrhidan Sands
- 100% of 48 C. edule from Lymington, Hampshire
- 74% of 359 specimens from Milford Haven

Life cycle

The adult digenean occurs naturally in the intestine of the oyster catcher Haematopus ostralegus occidentalis (Neumann)(Nicoll, 1906) and the common scoter Melanitta nigra (L.) (Jameson, 1902); Jameson and Nicoll, (1913).

The relationship between the metacercaria in the cockle and the adult has been established experimentally in ducklings by Bowers and James (1967). The first intermediate host has not been identified, but the metacercaria occur very commonly in C. edule, the second intermediate host.

Distribution of Meiogymnophallus minutus in various populations of Cerastoderma.

C. edule from the Crouch mixed cockle population were heavily infected by this parasite: 2,640 parasitised cockles were recorded from

2,696 examined, an incidence of 97.9%. No infected C. glaucum occurred in 2,401 individuals examined. The River Roach C. edule were infected at a 94.4 incidence, whereas no C. glaucum were parasitised.

The incidence of infection of other C. edule populations are listed below:

Locality	Number in sample	Percentage incidence of infection	C. glaucum also examined from same locality
Wexford Harbour	18	100.0	-
Salcolme, Devon	17	64.7	-
Portland, Dorset	31	83.9	31 C. glaucum no M. minutus
Poole, Dorset	8	100.0	8 C. glaucum no M. minutus
Portsmouth, Hampshire	34	96.7	3 C. glaucum no M. minutus
Whitstable, Kent	61	88.5	-
Southend, Essex (1968-9)	328	100.0	-
Maplin Sands, Essex	87	0	-
Tollesbury, Essex	32	100.0	-
Southend, Essex (May 1970)	500	100.0	-

No C. glaucum from any lagoon populations were infected; this parasite was absent from 359 individuals examined.

Discussion

Meiomymnophallus minutus has thus been shown to be extremely host specific in selection of the second intermediate host. Within the Cerastoderma, C. edule was invariably infected whereas no C. glaucum were found to be parasitised. There are several hypotheses which could

account for the complete absence of infection in this latter cockle from the mixed population. The hinge teeth organisation is slightly different in C. glaucum compared with C. edule (see Tebble (1966) figure 55, p. 105). Also, the ligament is compressed in C. glaucum, thus both factors could result in the exclusion of the metacercariae from the particular niche where encystment occur. Alternatively as the cysts surrounding the metacercariae are produced by the host tissue in C. edule, (Bowers and James, 1967), it could well be that C. glaucum is able to destroy the infective cercariae when the mantle epithelium is stimulated by their presence.

This parasite occurs at a high percentage incidence in the majority of C. edule populations examined. The only occasion that M. minutus was absent was in a sample collected at extreme low water springs (E.L.W.S) from Kaplin Sands, Essex. The shore is predominantly sandy and the gradient is very shallow resulting in a very long beach. This absence of infection is of interest, as 100% incidence has been found in C. edule collected from the middle shore at Southend, only a few miles distant. The only other recorded absence of this parasite is given by Bowers (1965) who failed to find M. minutus in C. edule from the Kyle of Tongue, a sandy estuary in North Scotland. It is unlikely that this Cerastoderma population consists of C. glaucum as this cockle has not been recorded in the area (see Section III), although this would explain the absence of the metacercariae.

Alternatively, the non-infection of these C. edule populations could be explained by the absence of the definite host, or by the absence of the first intermediate host. Local environmental conditions such as shore level may also regulate infection.

The definitive hosts, the oyster catcher H. ostralegus accidentalis and the common scoter, M. nigra, are both widely distributed over the whole of the British Isles (Peterson, Mountfort and Hollom, 1965). The first intermediate host has not however been determined. Gymnophallid life cycles usually involve a marine lamellibranch as the first intermediate host, (Stunkard & Uzmann, 1958); but James (1964), has recently described an exception Parvatrema homoeotecnum (James, 1964), in which the germinal sacs, cercariae and metercercariae occur within the gastropod, Littorina saxatilis (Olivi) subsp. tenebrosa (Montaqu). Bowers & James (1967) were unable to discover a littoral lamellibranch on Llanrhidian Sands with a furcocercous cercaria likely to be the first intermediate host, or to locate the developmental stage within C. edule, and conclude that a sub-littoral lamellibranch probably acts as the first intermediate host. They support this suggestion by the fact that the common scoter feeds upon sub-littoral bottom fauna.

M. minutus is found in C. edule populations living in estuaries e.g. The Crouch, Essex; the Adur, Sussex; The Dovey, Wales (Rees, 1939); and the Deucleddau, Pembrokshire, S. Wales (Bowers, 1965). It also occurs in cockle populations from muddy shores e.g. Chalkwell, Southend, Essex; Portsmouth, Hampshire; Milford Haven, Wales (Bowers, 1965); and from muddy-sandy shores of Southend, Essex; Whitstable, Kent; Poole, Dorset; Salcombe, Devon; Swansea Bay (Bowers, 1965) and Wexford Harbour, Eire. It is difficult to suggest a single bivalve which occurs sub-littoral to all these three types of shores. Furthermore, the Maplin sands cockles from E.L.W.S. would not be expected to be completely un-infected if the first intermediate host was a sub-littoral lamellibranch.

A common feature of the Kyle of Tongue and Maplin habitats is that both localities are sandy. It could be suggested that the first

intermediate host may well be a littoral mollusc living only in fine particulate or muddy substrates. The infective cercariae released from this mollusc would then only infect the littoral C. edule of the community living in the near vicinity. The shore at Maplin Sands is very long indeed, being some three miles from L.W.M.S. to L.W.N.T. compared with, at the most, one mile at Chalkwell, Southend. This suggests that shore level may play a part in determining infection. However the cockles from the Crouch and Roach estuaries were also collected from L.W.N.T. and these are highly infected. It may be that shore type which regulates the associated littoral fauna, and probably therefore the first intermediate host, is important in determining infection within the second intermediate host C. edule. (For further comments and suggestions for a possible first intermediate host for this digenean, see Appendix V).

II Incidence of the Turbellarian Paravortex cardii (Hallez, 1909)

Description (See plate 5.)

This parasitic, Rhabdocoel, turbellarian occurs in the intestine of Cerastoderma edule, and the same or different species have been recorded from several other lamellibranchs. It is viviparous and numerous young are often found within one adult. The size is very variable, adults averaging 0.39 x 0.25 mm - 0.95 x 0.5 mm. Hallez (1909) records up to 40 young in maximum sized P. cardii of 1.0 x 0.3 - 0.4 mm. The largest Paravortex noted in this study originated from Scrobicularia plana, and measured 1.5 x 0.36 mm and contained 102 paired young, the diameter of each young pair being 0.09 mm.

Plate 5

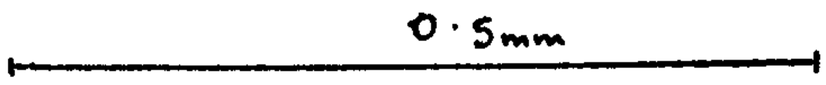
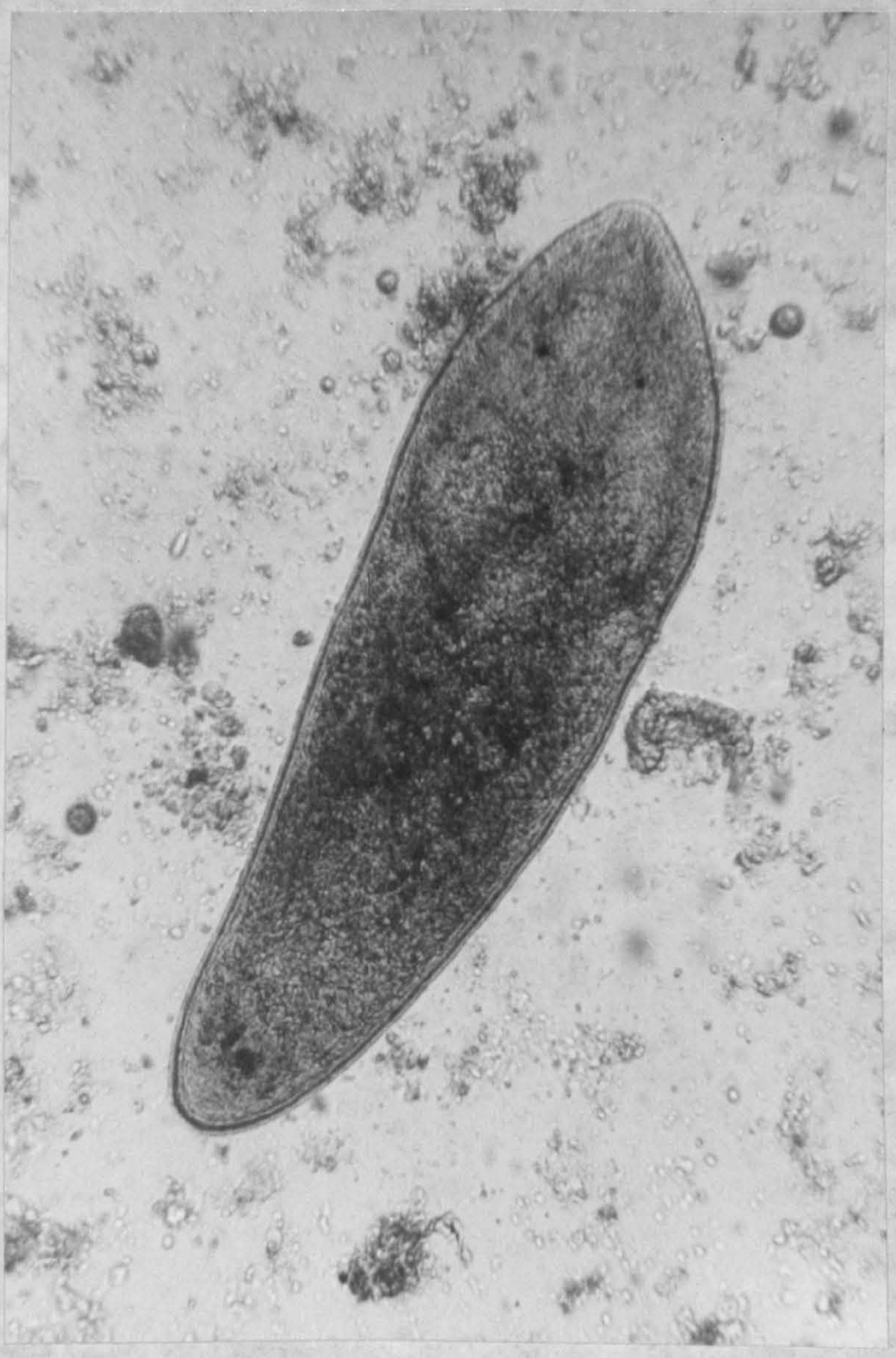


Plate 5 - Photograph of the Rhabdocoel Paravortex cardii from the intestine of the Cerastoderma.



Paravortex is characterised by the presence of paired, bean shaped eye-spots anteriorly. When released from the intestine or digestive gland P. cardii is very active, moving by ciliary action in a circular fashion. The genus Paravortex was established by Wahl (1906) for the Rhabdocoel living in the intestine of Scrobicularia plana (da Costa).

Speciation within the parasitic Rhabdocoela

Hallez (1909) divides Paravortex into three species; P. Cardii, P. scrobicularinae and P. tellinae separating them mainly on the basis of genital pore position. He records P. cardii only in C. edule; P. Scrobicularinae in Scrobicularia plana and a Venerupis species; and P. tellinae in Tellina sp. and a Solen sp. This latter Paravortex he states to be twice as large as P. cardii and P. scrobicularinae. Basically the differences between P. cardii and P. scrobicularinae are as follows:

From Freeman (1957)

Paravortex species

Character	P. cardii	P. scrobicularinae
Colour	Yellow-white	Reddish tint
Maximum size	1 mm.	1.2 mm.
Genital pore	⅓ of body length from ant. end	End 2/5 of body
Ovaries	Bicorniculate	Longitudinally placed ovaries
Embryo length upon hatching	0.088 mm.	0.08 mm.

Thus it would appear that there is sufficient evidence to support at least two species of Rhabdocoel in the intestine of bivalves.

However, Bowers (1965) does not differentiate, into different species the Rhabdocoels found in a variety of lamellibranchs S. plana, C. edule, Hiatella artica (L.) and Pharus legumen (L.), calling them all P. cardii.

The Rhabdocoel Graffilla (= Paravortex) gemellipara (Linton, 1910) is also recorded by Leigh-Sharpe (1933) attached to the body surface within the mantle cavity of C. edule from Plymouth. Chrenko (1934) supported this observation finding G. gemellipara on the body surface and in the testis of C. edule, whereas he records P. cardii as occurring in the ovary of C. edule. He compares these two Rhabdocoels; G. gemellipara is twice as large as P. cardii and moves by creeping in contrast to the circular movement displayed by P. cardii. G. gemellipara was not found in this study.

Previous Records of P. cardii

- Lebour (1904) describes a 'sporocyst' which was undoubtedly this Rhabdocoel, occurring in 12 of 20 C. edule examined from the Northumberland coast.

- Nicoll (1906) also mistook this Rhabdocoel for the 'sporocyst' above. In C. edule from St. Andrews, Scotland. Rarely more than six individuals occurred in each host, and an incidence of 80% is recorded in this cockle population.

- Hallez (1909) in C. edule from Le Portel, Boulogne-sur-Mer, at 47% incidence.

- Chrenko (1934) - P. cardii in one of 12 C. edule examined from Tamar estuary, Devon.

- Atkins (1934) - Incidence varied from 23-100% in Plymouth region, but sample numbers were invariably low:

General site description	Location of site	Number of C. edule examined	Incidence of Infection
Marine	Millbrook & St. Johns Lake, River Tamar	10 + 3	100%
Marine	Stone House, Pool, River Tamar	13	92%
Estuary	St. Germans (Lynher River)	14	85.7%
"	Neal Point, junction of River Tamar & Tavy	10	40%
"	Kingsbridge, Salcombe estuary	17	23%
Marine	Millbay, Salcombe estuary	6	0%

Rees (1939) - Present in C. edule from Dovey estuary, Wales

Cole (1956) - Recorded as common in gut of C. edule from Conway, N. Wales.

Hancock & Urquhart (1965) - 13% infection in C. edule from Llanrhidian Sands, S. Wales.

Bowers (1965) - This parasite was recorded in C. edule as follows:

General site description	Locality	Number examined	Incidence of Infection
Sandy estuary	Llanrhidian Sands	10,500	92%
Muddy & rocky shore	Swansea Bay	503	90%
Muddy shore	Milford Haven	359	36%
Muddy estuary	Lymington, Hampshire	48	33%

Also recorded by Bowers in: Hiatella arctica (L.) - 6% of 150 specimens examined

Scrobicularia plana (da Costa) - 50% of 21 specimens examined

Pharas legumen (L.) - 16% of 32 specimens examined.

Occurrence of Paravortex cardii in various Cerastoderma populations

Only P. cardii was found within the Cerastoderma. This Rhabdocoel occurred in both C. edule and C. glaucum from the Crouch mixed cockle population. Of 2,447 C. edule examined only 37 were infected, an incidence of 1.5%. In contrast 271 parasitised C. glaucum were found in 2,188 examined, a 12.4% infection incidence. The River Roach estuarine cockles were also infected, C. edule at 7.9% incidence and C. glaucum at 26.1% incidence. Therefore, in both mixed cockle populations a higher incidence was found in C. glaucum compared with C. edule.

No. P. cardii occurred in lagoonal populations of C. glaucum. Single very small Rhabdocoels probably of the genus Paravortex were however noted in the mantle cavity fluid of two C. glaucum from Gosport lagoon, Hampshire. Because of the absence of adults and the very small size of these two turbellarians, they were probably no P. cardii.

The other littoral C. edule populations examined yielded a variety of infection incidences as follows:

Shore type	Locality	Date examined	Nos. of C. edule examined	Percentage Incidence of Infection
Very muddy	Portsmouth, Hants	May 1969	34	20.6%
Muddy	Southend, Essex	Jan. 1969	104	10.6%
"	" "	Feb. 1969	124	11.5%
"	" "	May 1969	71	22.7%
Muddy - sand	Wexford Harbour, Eire	Aug. 1969	18	16.7%
Sandy (little mud)	Maplin Sands, Essex	July 1969	87	5.7%

Shore type	Locality	Date examined	Nos. of C. edule examined	Percentage Incidence of Infection
Sandy (little mud)	Whitstable, Kent	Dec. 1968	61	6.6
Sandy (little mud)	Malcolme, Devon	March 1969	17	5.9
Sandy	Portland, Dorset	Aug. 1968	31	0

Hallez (1909) studied P. cardii in a population of C. edule, through a yearly cycle, and found the incidence to be remarkably stable. Thus, although the samples above were taken at different times through the year, some conclusions as regards to abundance can be drawn. Infection incidences were greatest in C. edule from muddy non-estuarine habitats. The substratum type probably has some regulatory effect upon the free living, dispersal phase of the life cycle. A Paravortex species was noted within the egg capsule of Phyllodoce maculata during this survey, and thus another host may play a part in the unknown complete life cycle of Paravortex cardii.

Salinity, as well as substrate, may well regulate the distribution and abundance of this species. Bowers (1965) (see earlier) records a much lower incidence in estuarine localities compared from more saline environments and this has been substantiated in this investigation. The slightly higher average salinity of the River Roach compared with the River Crouch may account for the higher observed incidence of P. cardii in both the Roach Cerastoderma populations compared with the Crouch cockles.

The density of the cockle host may also be important as there is some evidence that low density C. edule populations are relatively uninfected compared with more dense cockle populations. P. cardii thus

parasitised both C. edule and C. glaucum, occurring more abundantly in numbers and infection incidence in C. glaucum from the mixed Cerastoderma populations examined.

III Incidence of the Protozoan Ciliate Trichodina sp.

Order - Peritrichida (Stein, 1859)

Family - Urceolaridae (Dujardin, 1841)

Sub-family - Trichodininae (Raabe, 1963)

Genus - Trichodina (Ehrenberg, 1838)

Description

Round, saucer shaped, hemispherical ciliate with rows of circumferential cilia. Internal circular skeleton composed of interlocking denticles (see fig. 1 and plate 6). Found, often abundantly, within the mantle cavity fluid of bivalves.

Previous Records

Nicholl (1906) recorded swarms of Trichodina sp. in the mantle cavity fluid of C. edule from St. Andrews, Scotland.

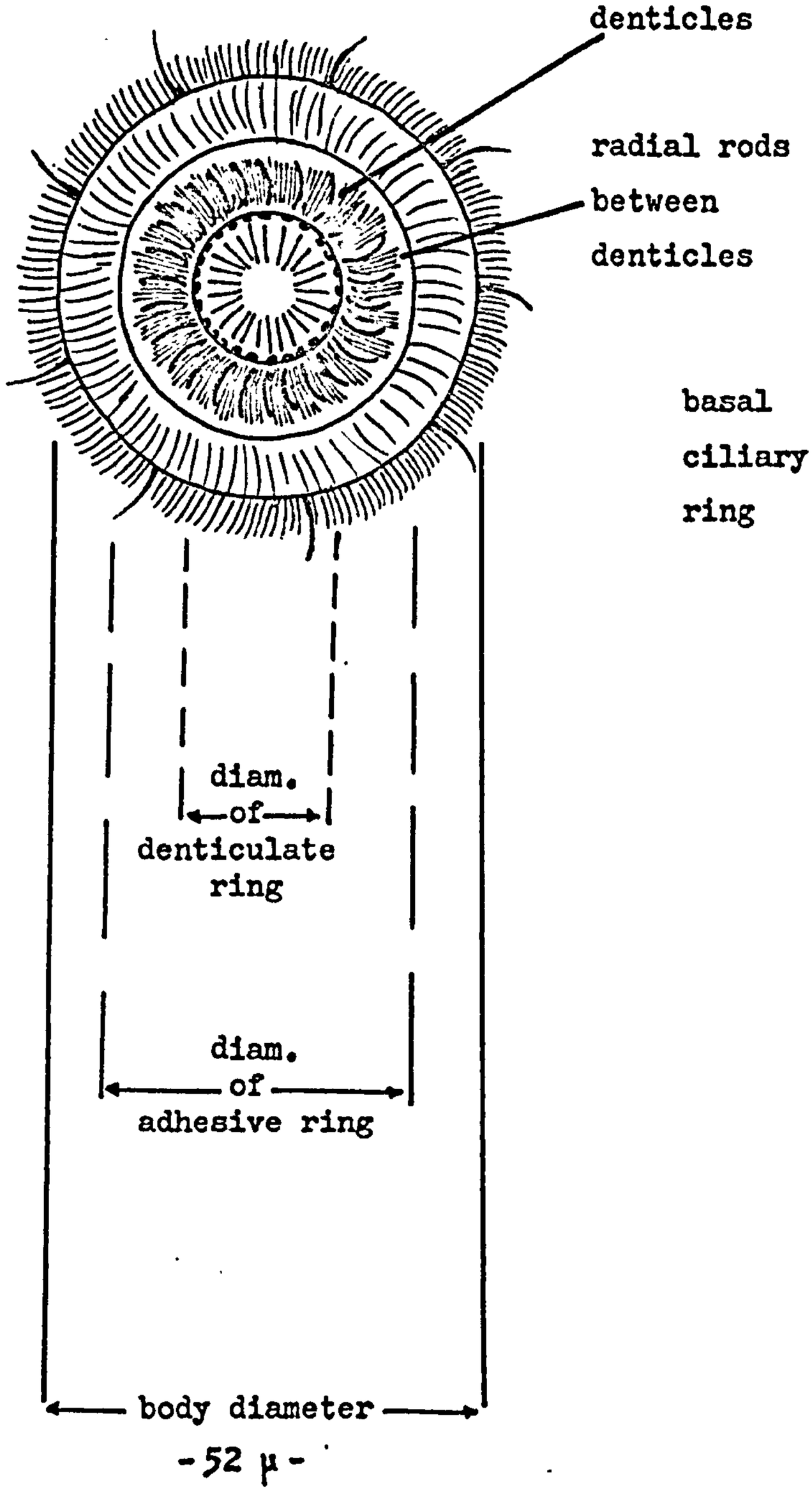
Trichodina (= Cyclochaeta) cardii was described briefly by Delphy (1938), at 50% incidence in the mantle cavity of C. edule from Arcachon, France. His brief description is regarded to be inadequate by Raabe & Raabe (1959) who consider the name Cyclochaeta cardii Delphy as a nomen nudum.

Cole (1956) noted that T. cardii was common in C. edule from Conway, N. Wales.

Raabe & Raabe (1959) describe two trichodinids from C. edule (this cockle noted to be C. lamarcki (= glaucum) by Fenchel, 1965) from the Polish coast (see table 5).

Diagram 1

Scopula of Tricodina sp. from Cerastoderma edule



Side - view showing flattened body.

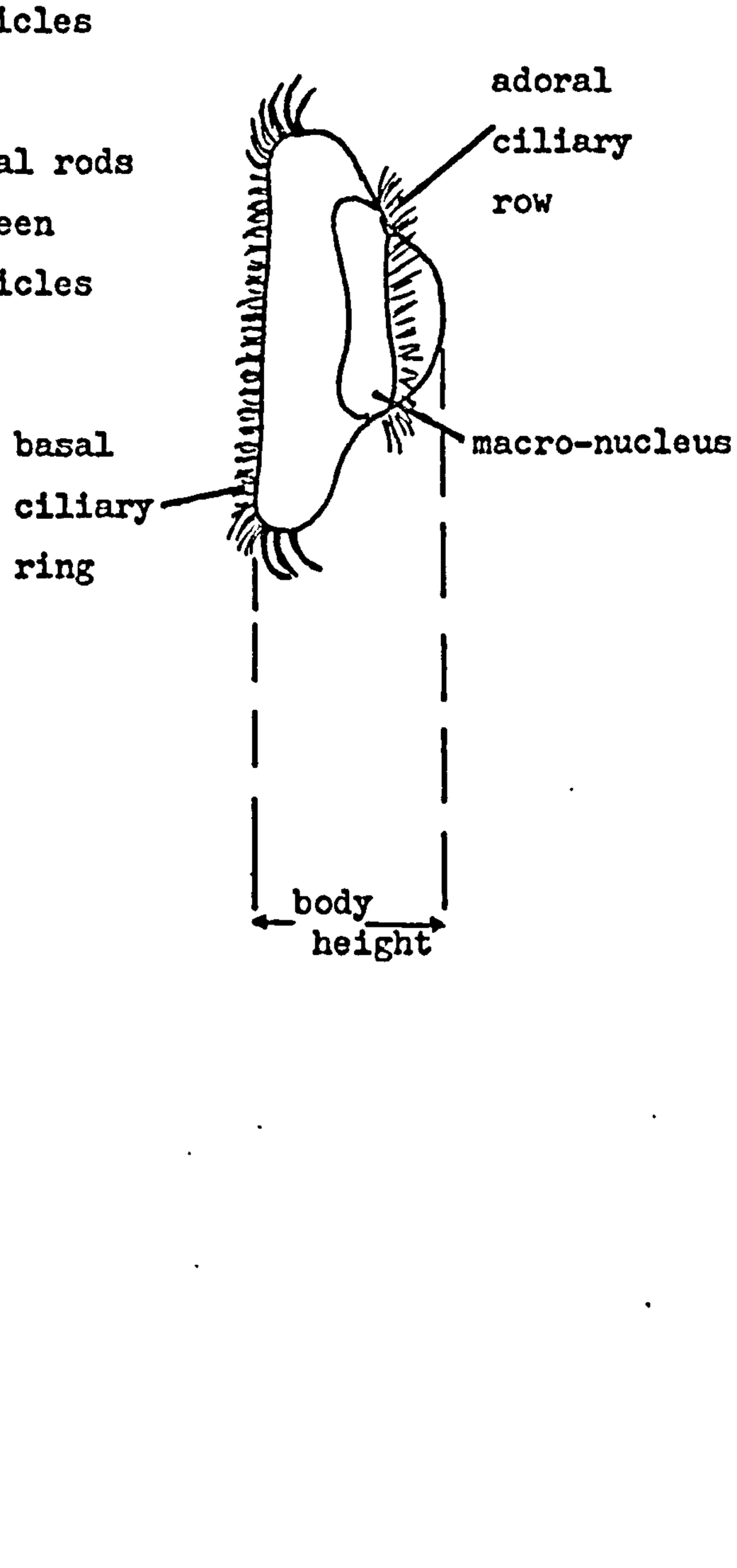


Plate 6

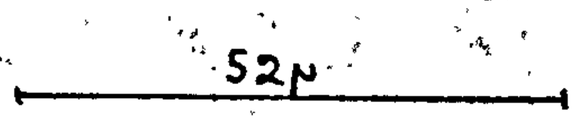
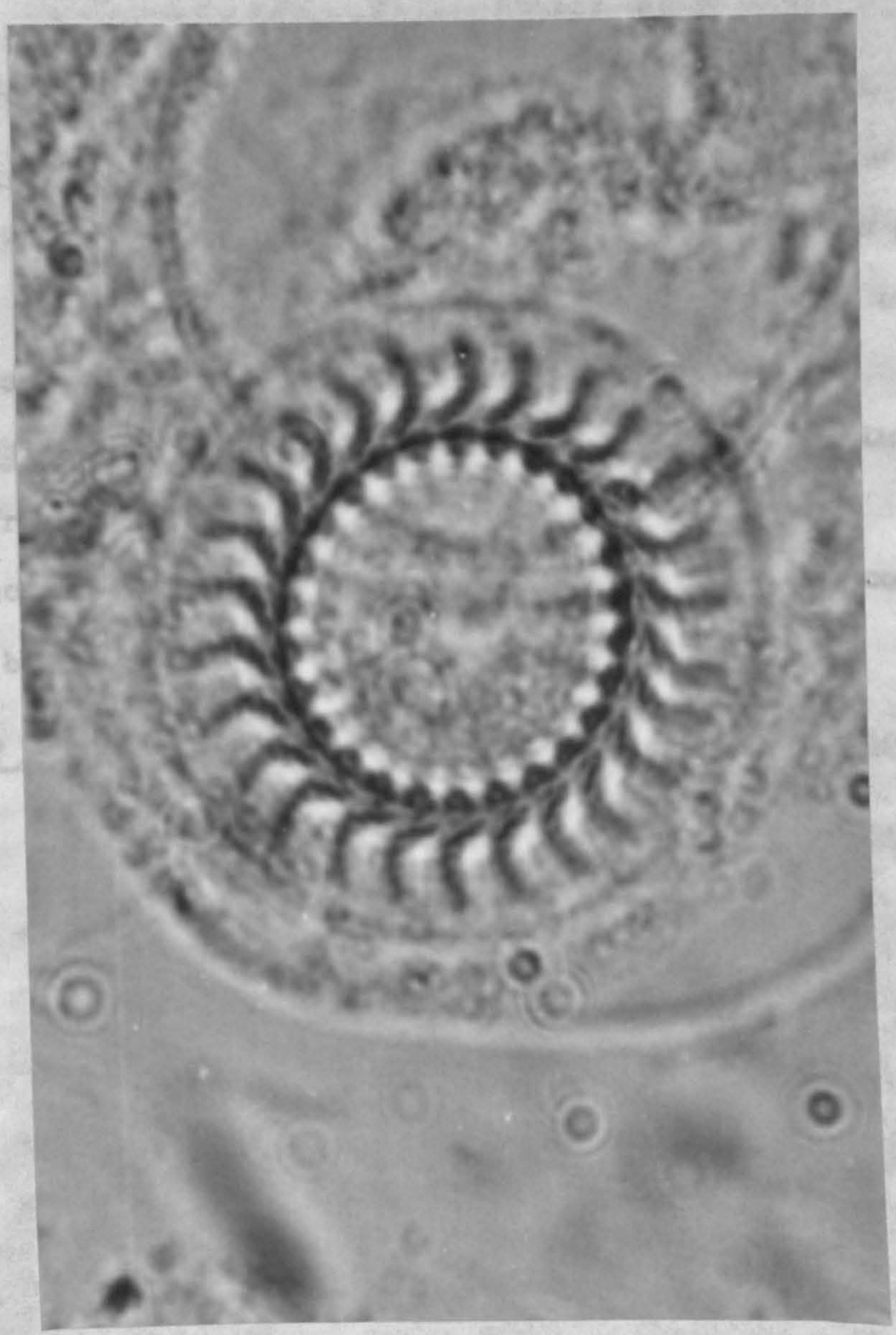


Plate 6 - Showing denticular ring of Trichodina sp.

from C. edule.



Hancock and Urquhart (1965) - as T. cardii in 12% of 438 C. edule of various ages examined from Llanrhidian Sands, S. Wales.

Fenchel (1965) describes two Trichodina species, one of which he equates with a species previously recorded by Raabe & Raabe (1959), from C. edule and C. lamarcki (= glaucum, - see table 5 below.

Bowers (1965) records T. cardii in 20% of C. edule from Swansea Bay, and in 50% of 10,500 cockles from Llanrhidian Sands, S. Wales. He also records T. cardii from 2% of 20 Macoma balthica from Swansea Bay, but this Trichodina was not specifically identified and may be a different species.

Distribution of Trichodina in the British Cerastoderma

Trichodina species occurred within both cockle types from the Crouch mixed population. 82 C. edule examined in the summer of 1969 yielded an incidence of 56.1%, whilst 41.1% of 90 C. glaucum, collected at the same time, also contained Trichodina within the mantle cavity.

No Trichodina species were found in the mantle cavity fluid of any C. glaucum from any lagoon populations.

Incidences within littoral C. edule populations varied considerably (see below) but the populations were invariably infected.

Incidence of Trichodina in various littoral C. edule populations

Locality	Date	Incidence of Trichodina sp.
Southend, Essex	Jan. 1969	0.1%
" "	Feb. 1969	3.1%
" "	May 1969	3.6%
" "	July 1969	11.5%
Whitstable, Kent	Sept. 1968	10.0%
Portsmouth, Hants	May 1969	7.0%

Locality	Date	Incidence of Trichodina sp.
Crouch, Essex	May 1968 - Sept. 1969	0 - 90%
Salcolme, Devon	March 1969	29%
Tollesbury, Essex	Oct. 1969	38%
Wexford Harbour, Eire	Aug. 1969	66.7%
Poole, Dorset	May 1970	62%

As can be seen from the Southend data (and also noted in the Crouch cockles), the lowest incidence occurred during the winter months, whilst the highest were found in the summer and autumn. Lagoon cockles are not infected by Trichodina sp. whilst the stickleback Gasterosteus oculeatus from the same habitat is usually infected by Trichodina domerguei domerguei (Wall, 1897) (H.J.G. Dartnall, personal communication).

This tends to suggest that the Trichodina found in C. edule and C. glaucum from littoral locations is different from T. domergoi f. cardii (Raabe & Raabe, 1959).

The sizes and characters of the Trichodina from four Cerastoderma populations are shown below:

Cockle host & locality	Number of Trichodina examined	Body	Diameter of Adhesive disc	Diameter of Denticulate ring	Nos. of Denticles	Nos. of radial rods/ denticle
C. edule (Wexford)	7	66.5	43.7	22.7	25(24-26)	-
C. edule (Portsmouth)	10	64.7	44.4	21.0	25(22-27)	-
C. edule (Crouch)	9	55.7	39.2	20.3	23(21-25)	7(5-9)
C. glaucum (Crouch)	9	52.5	35.3	17.5	21(20-24)	-

Table 5 Comparison of Recorded Trichodina Species from the Cerastoderma

Morphological Character	1. T.cardii (Delphy, 1938)	2. T.cardiorum (Raabe & Raabe, 1959)	3a. T.domerguei (Wallengren) f.cardii (Raabe & Raabe 1959)	3b. T.polandiae (Fenchel, 1965) (regarded by Fenchel to be indentical with 3a but sufficiently different from T.domerguei, found on various fishes, to warrent a new species name.	4. Trichodina sp. (Fenchel, 1965
Body Size	60 - 80 μ	75 μ (range 54-90μ)	38μ- 50μ	52μ (47-60μ)	52μ(44-56)
Height	30 - 40 μ	20 μ	20μ	-	-
Diameter of adoral ring	—	45μ- 65μ	36μ	-	-
Diameter of denticulate ring		22 μ (16-26μ)	25μ (21-28μ)	25μ (21-29μ)	21μ (20-24μ)
Denticle Nos.	—	25 (24-29)	Commonly 20-21 (Range 18-22)	18 (19-23)	24 (22-25)
No. of Radial rods/Denticle	—	—	—	7 - 10	About 5
	C.edule*	C.glaucum	C.glaucum	C.glaucum	C.edule
	in 50% of cockle population from Arcachon, French Atlantic Coast. Probably high salinity water	Exclusively in young cockles up to 5 mm long most commonly in specimens 2-3 mm long. 50% incidence on Polish Baltic Coast - in low salinity water	In small cockles In lower salinity areas than T.cardiorum	100% incidence in small C.glaucum from Askö, Poland. A little lower incidence in larger specimens. Absent from Scandinavia waters	100% of C.edule from Øresund, Sweden. Higher salinity water than previous species

*Recorded as C.edule but the Arcachon basin has been shown by Russell (1969) to harbour both C.edule and C.glaucum

Comparing Trichodina from the Crouch Cerastoderma the ciliates found in the mantle cavity of C. glaucum generally appeared smaller than those found in C. edule. On the other-hand the individuals from the Crouch C. edule were also smaller than those found in other cockle populations. It may be found that salinity and perhaps other factors affect the size of Trichodina in different host populations of C. edule.

Considering the above measurements and comparing them with those shown on table 5, it would seem that the Trichodina sp. of Frenchel (1965) from Swedish C. edule, best fits the Trichodina found in the British Cerastoderma. The fact that Trichodina was absent from lagoonal populations of C. glaucum indicates that this ciliate is not tolerant of stagnant brackish conditions. It is, however, a species tolerant of salinity fluctuations which occur in estuaries.

Trichodina sp. therefore occurs in both Cerastoderma types from an estuarine environment.

IV Presence of the Copepod Crustacean - Hermanella (Paranthessius) rostrata (Canu, 1891)

(for key of the Paranthessius group of cyclopoid copepods - see stock, 1953)

Description (see plate 7)

This cyclopoid copepod is characterised by having a well marked, incurved rostram. The anterior antenna (antennule) is 7-articulated and independent of the cephalothorax. The antenna is strongly developed, 4-articulated and imperfectly prehensile - see diagram 2 below. Cann, 1891 notes that the fourth pair of thoracic limbs bear a three articulated

Plate 7

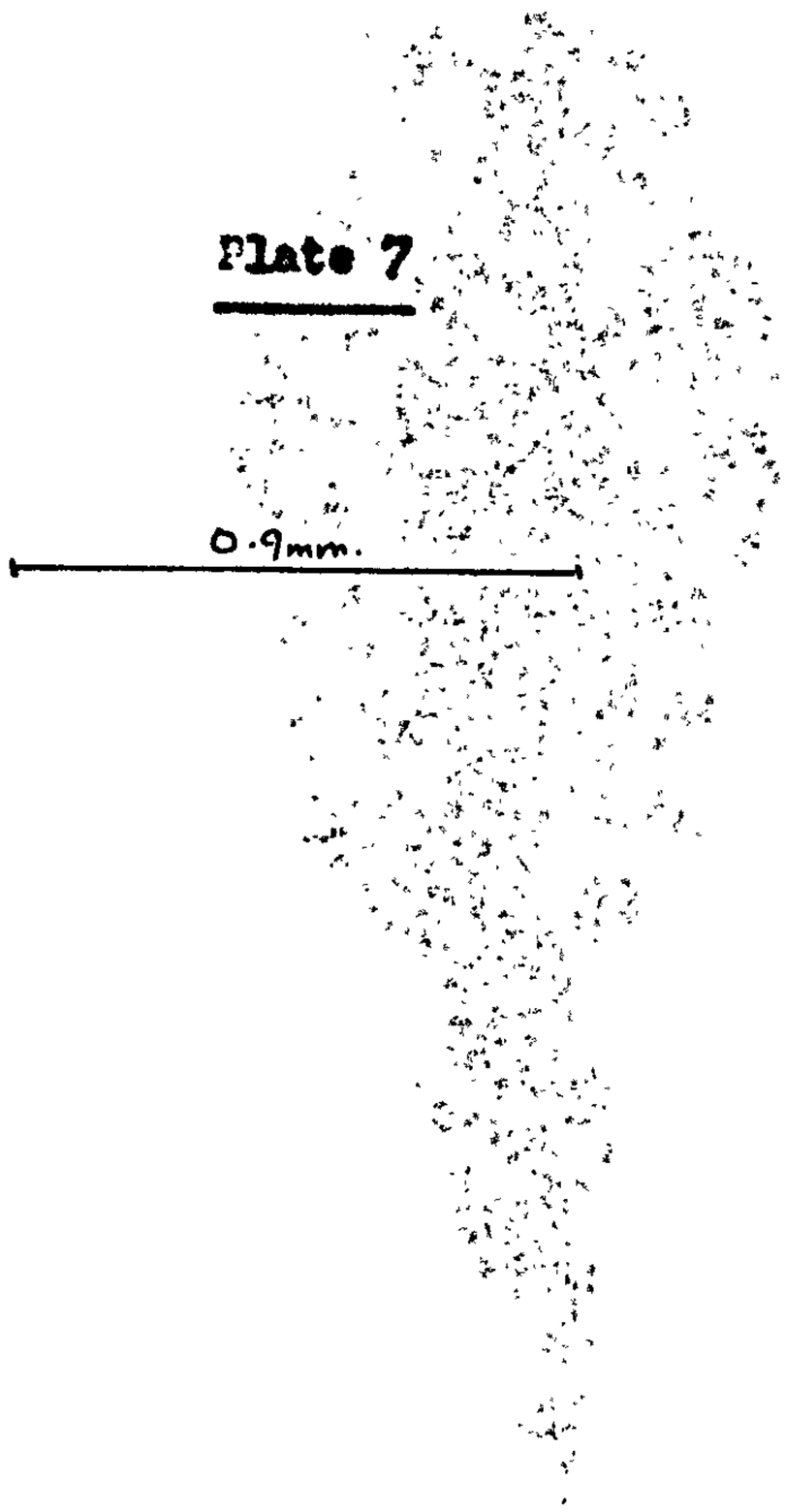


Plate 7 - Photograph of the copepod Herrmanella rostrata from C. edule.

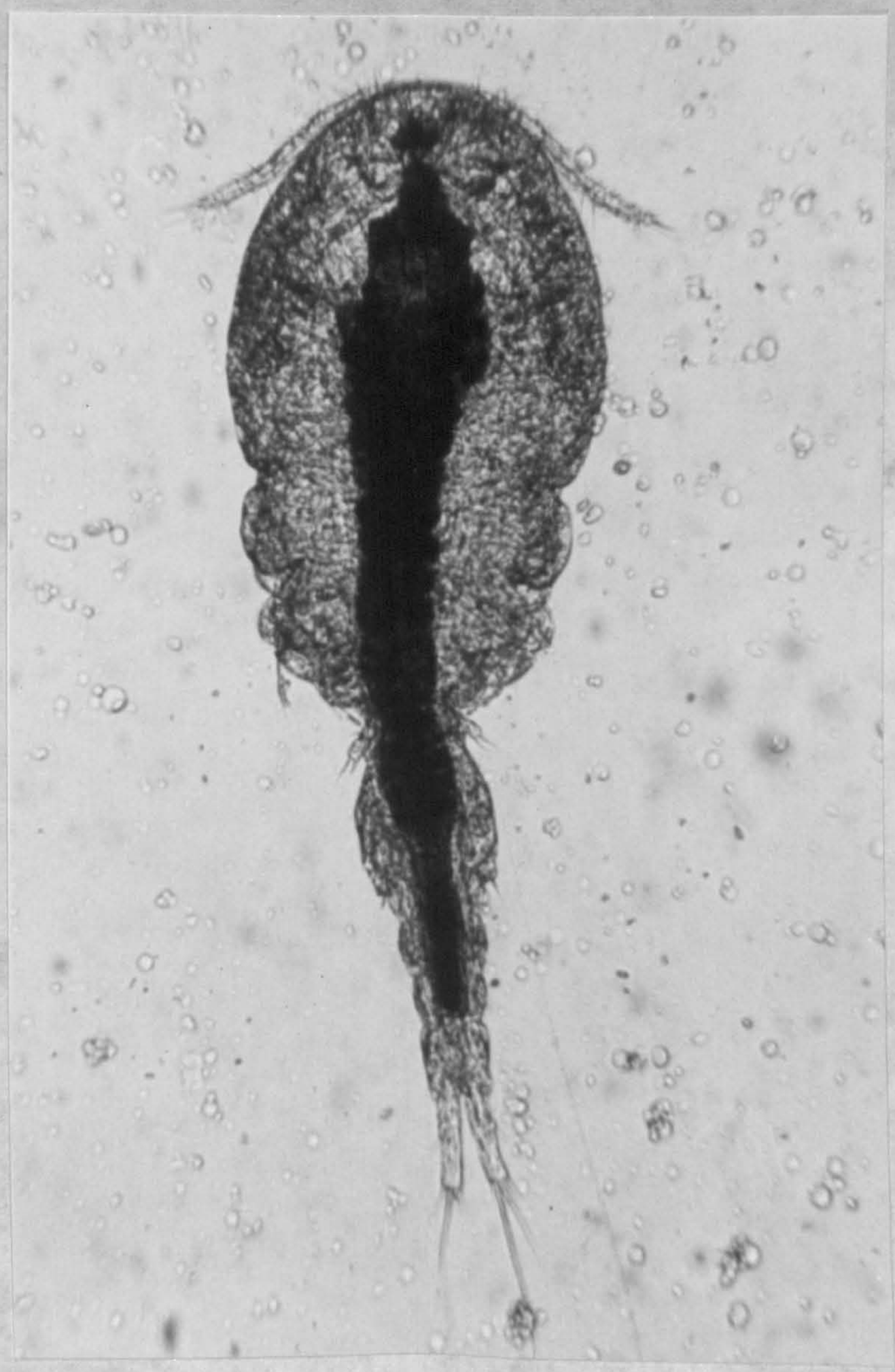
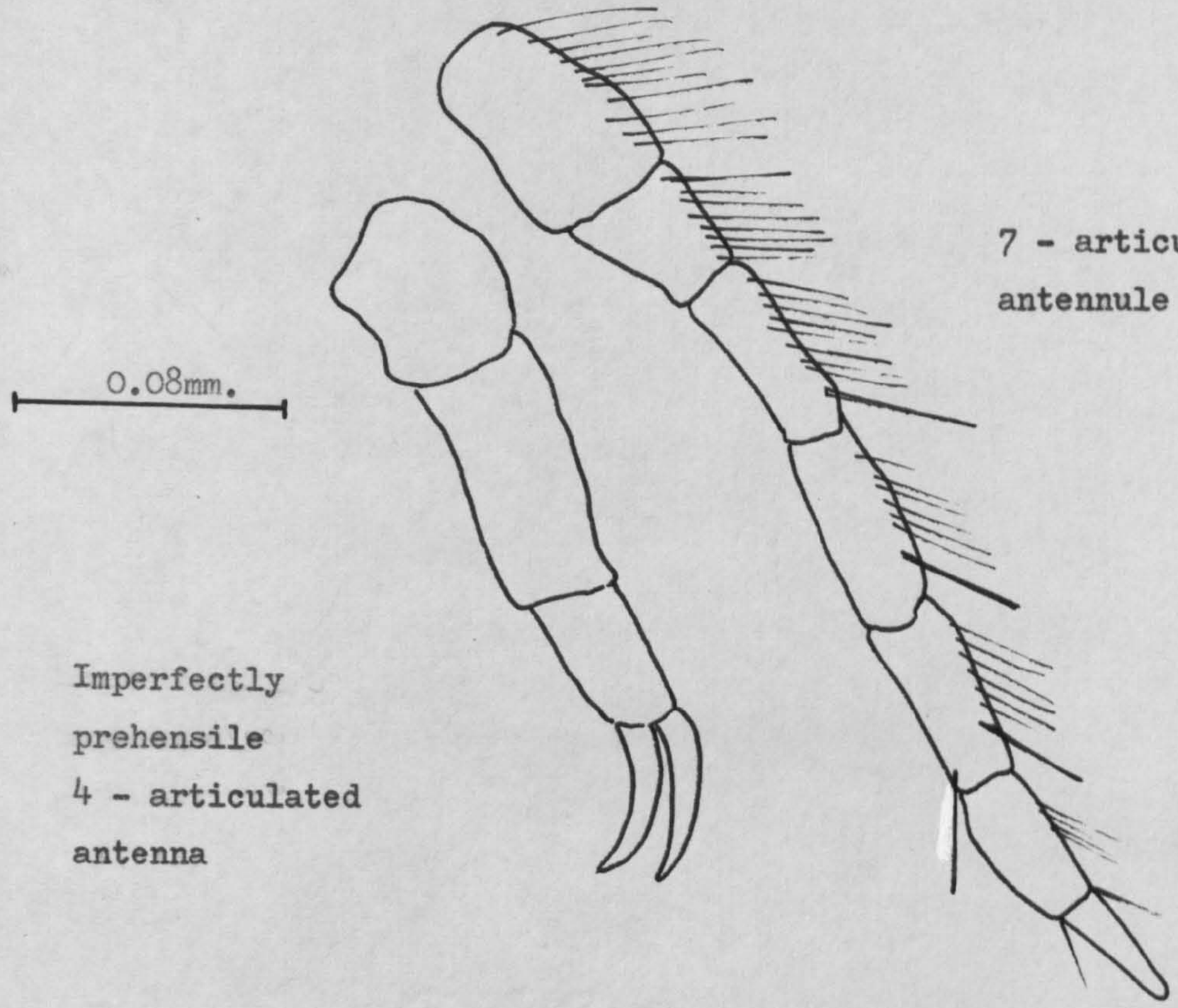
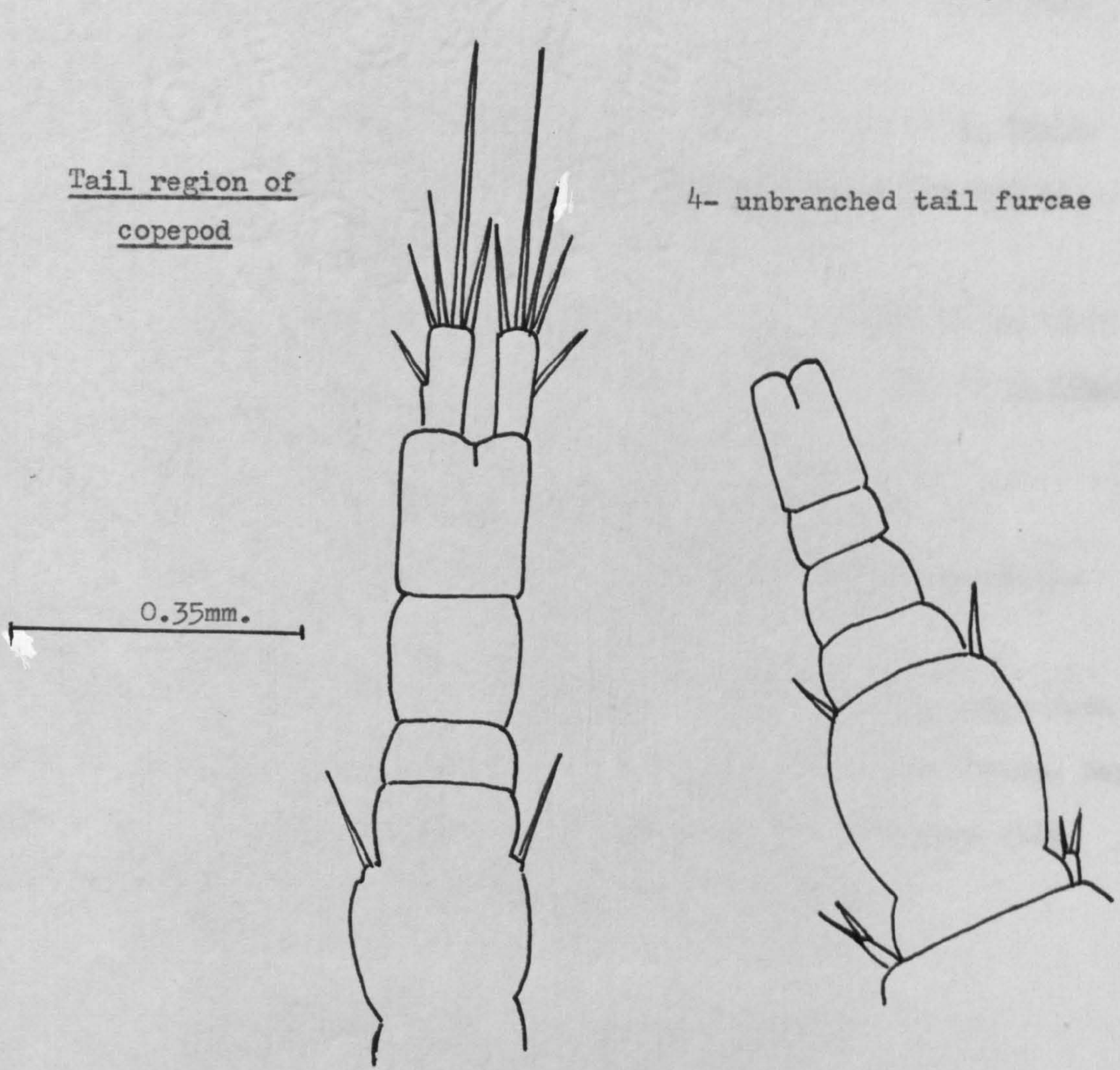


Diagram 2 - First appendages and tail section of the Copepod Hermannella rostrata.



Tail region of copepod



endopodite. He first described this semi-parasitic copepod as Hermannella rostrata the name Lichomolgus agilis being subsequently ascribed by Scott (1892).

The sizes obtained for this copepod are as follows:

Maximum length of body + tail	=	1.04 - 2.68 mm.
Maximum width of cephalothorax	=	0.80 - 0.96 mm.
Length of antennule	=	0.24 - 0.52 mm.
Body length	=	0.80 - 2.18 mm.
Length of longest tail furea	=	0.24 - 0.52 mm.

Previous records

Canu (1891) records this copepod in C. edule (L.), Lactra corallina (L), and Chlamys opercularis (L.) from the French coast.

Scott (1892) and Thompson (1893) note this copepod (as L. agilis) in C. edule from Morecombe Bay, Lancashire.

Frazer (1932) found H. rostrata in the mantle cavity of C. edule, again from Morecombe Bay, and also in tow-nets from above the cockle beds.

Leigh-Sharpe (1933) records this copepod in the testis of C. edule from Plymouth and Atkins (1934) reports an incidence of 100% in C. edule from six sites in the Plymouth area, Devon.

Cole (1956) in C. edule from Conway, N. Wales.

Hancock and Urquhart (1965) found a maximum of 83% of Llanrhidan C. edule infected.

Bowers (1965) records an average incidence of 50% in C. edule from Llanrhidan Sands and Milford Haven, and 80% in C. edule from Swansea Bay, S. Wales. The copepod was absent in cockles examined by Bowers from Lymington, Hampshire and Kyle of Tongue, North Scotland.

Presence of H. rostrata in various cockle populations

This copepod was only found in the last two samples of C. edule collected from the Crouch mixed population, during August and September 1969. Four infected individuals occurred in 35 C. edule examined in these samples. Thus, no copepods were discovered in either cockle during the major portion of this survey. This symbiont is rare in the Crouch estuary and therefore no conclusions can be drawn as regards its host selection.

However, no lagoon populations of C. glaucum were infected, whilst a variable incidence was recorded in littoral C. edule populations. The copepod was found at 1 - 10% incidence in Southend C. edule during the major part of this survey, but it occurred at 71% incidence in a nearby Essex C. edule population at Tollesbury. In the summer of 1970 a 90% incidence was noted in the 500 Southend cockles examined. It was absent from the Whitstable cockle population, but occurred in Portsmouth cockles at 2.9% incidence; in Poole Harbour C. edule at 67% incidence; in Malcolme, Devon C. edule at 88.2% (average of 3 per cockle (range 1 - 7)), and Wexford Harbour cockles at 100% incidence (average of 3 per cockle, (range 1 - 6)).

This copepod therefore infects littoral C. edule, but is absent from marine lagoon populations of C. glaucum. It would seem therefore, that H. rostrata cannot tolerate permanent, salinity reductions, which usually occur in lagoons, or large temporary fluctuations which are found in estuaries, e.g. the Crouch. It would seem therefore, to be a relatively stenohaline copepod.

V Incidence of other symbionts occasionally encountered within the Cerastoderma

During this investigation three other symbionts were also noted:

1. Pinnotheres sp. (= probably pisum Pennant) was found in the mantle cavity of several Cerastoderma. Infected C. edule occurred at: Minnis Bay, North Kent at E.L.w.S. mark in large specimen; at Portsmouth, Hampshire; and Portland, Dorset. Two C. glaucum, one from each of the Essex Crouch and Roach estuaries were also infected.

2. A gymnophallid cercaria (or metacercaria) was occasionally found between the mantle and shell of C. edule and more rarely in C. glaucum from the mixed Crouch population (for further details see Appendix IV).

3. A sample of 72 C. glaucum from Sheerness lagoon, Isle of Sheppey, Kent were collected on the 17th June 1969. Within the mantle cavity of 55.6% (42 individuals) occurred swarms of rotifers of the genus Synchaeta. They were also present, free in the water and thus their presence in the mantle cavity fluid may have been accidental. With reference to Holloway (1949), the rotifer was identified as Synchaeta littoralis (Rousselet). A further cockle sample from this lagoon collected on the 25th July 1969 was uninfected by the rotifer. Within the mantle cavity of 9.2% of the sample of C. edule from Maplin Sands were found Synchaeta sp. probably Synchaeta littoralis.

VI Comparison of the symbiont fauna of C. edule and C. glaucum from the mixed cockle populations of the River Crouch and Roach, Essex

As the two cockles are very close relatives of the same genus, the symbiont fauna of the two types would be expected to be very similar.

The overall infection of the Crouch and Roach mixed Cerastoderma populations are shown in table 6.

The pattern found in the Crouch cockles is generally supported by the infections found in the Roach Cerastoderma. The metacercaria Meiogymnophallus minutus is entirely absent from both populations of C. glaucum, while the bucephalid Cercaria B. haimeana is recorded only once in the Crouch C. glaucum.

On the whole, C. edule is more highly infected by first stage larval Digenea than C. glaucum; 13% of C. edule being castrated compared with 0.4% in C. glaucum, the difference being chiefly due to the bucephalid parasite. A less important parasite, the Rhabdocoel Paravortex cardii, on the other hand, is more abundant and occurs at a higher incidence in C. glaucum than C. edule.

There is thus considerable differences in the symbiont fauna of the two cockles collected from a common environment.

Discussion

Host specificity in digenetic trematodes is a complex phenomenon, both physiological and ecological specificity acting in the selection of hosts. Specificity is a fundamental characteristic of parasites, but it is seldom absolute (Cameron, 1964).

Even when a parasite is apparently limited to a single host there may be other potential hosts which it could infect if it were exposed to them. Thus, normally in land-locked lagoons C. glaucum would not be able to form part of the cycle required for the perpetuation of a trematode life cycle with an adult stage in the intestine of a deep sea fish, because the fish never occur in the lagoon. Therefore, Cercaria lepidopedon rachion and Cercaria Bucephalopsis haimeana are automatically precluded

TABLE 6 Summarised Symbiont Fauna of C.edule and C.glaucum from the Mixed Cockle Populations of the Rivers Crouch & Roach Estuaries, Essex

Cockle Type	No. of cockles examined	Digenea using the Cockle as first indeterminate host			Digenean using the cockle as 2nd indeterminate host	Percentage incidence of the Rhabdocoel Paravortex cardii	Symbionts of the mantle cavity		
		Percentage incidence of Cercaria B.haimeana	Percentage incidence of Cercaria dichotoma	Percentage incidence of Cercaria Lepidopedon rachion	Percentage incidence of metacercaria of Meiogymnophallus minutus		Presence of Trichodina sp	Presence of Herrmanella rostrata	Presence of Pinnotheres pisium
Crouch C.edule	2696	11.8	0.74	0.07	97.9	1.5	Present	Present	-
Crouch C.glaucum	2401	0.04	0.25	0.12	-	12.4	Present	-	Present
Roach C.edule	89	6.7	2.3	-	94.3	7.8	(not recorded)	-	-
Roach C.glaucum	23	-	-	4,3	-	20.7	(not recorded)	-	Present

UNIVERSITY OF LONDON

B.A./B.A. HONOURS EXAMINATION 1970

for Internal and External Students

LATIN

Unseen Translation from Greek

Tuesday, 9 June: 10 to 1

Translate into English:

(*a*)

Βουλὴν δὲ πρῶτον μεγαθύμων ἴζε γερόντων
Νεστορέῃ παρὰ νηῒ Πυλοιγενέος βασιλῆος·
τοὺς ὅ γε συγκαλέσας πυκινὴν ἀρτύνετο βουλήν·
" κλῦτε, φίλοι· θεῖός μοι ἐνύπνιον ἦλθεν Ὄνειρος
ἀμβροσίην διὰ νύκτα· μάλιστα δὲ Νέστορι δίῳ
εἶδός τε μέγεθός τε φυήν τ' ἄγχιστα ἐώικει·
στῆ δ' ἄρ' ὑπὲρ κεφαλῆς καί με πρὸς μῦθον ἔειπεν·
" εὕδεις, Ἀτρέος υἱὲ δαΐφρονος ἱπποδάμοιο·
οὐ χρὴ παννύχιον εὕδειν βουληφόρον ἄνδρα,
ᾧ λαοί τ' ἐπιτετράφαται καὶ τόσσα μέμηλε·
νῦν δ' ἐμέθεν ξύνες ὦκα· Διὸς δέ τοι ἄγγελός εἰμι,
ὃς σεῦ ἄνευθεν ἐὼν μέγα κήδεται ἠδ' ἐλεαίρει·
θωρῆξαί σε κέλευσε κάρη κομόωντας Ἀχαιοὺς
πανσυδίῃ· νῦν γάρ κεν ἕλοις πόλιν εὐρυάγυιαν
Τρώων· οὐ γὰρ ἔτ' ἀμφὶς Ὀλύμπια δώματ' ἔχοντες
ἀθάνατοι φράζονται· ἀπέγναμψεν γὰρ ἅπαντας
Ἥρη λισσομένη, Τρώεσσι δὲ κήδε' ἐφῆπται
ἐκ Διός· ἀλλὰ σὺ σῇσιν ἔχε φρεσίν."

HOMER, *Iliad*, ii, 53–70.

HUL 70/75 2/27/200+225

Turn over

from lagoon cockles. On the other hand, Cercaria dichotoma can occur in lagoon cockles, because the definitive host, a duck, may frequent the lagoon during the winter months. Also, the absence of a wide selection of other intermediate hosts in such pools as well as the limited choice of final definitive hosts, greatly reduces the life-cycles available for digenetic trematodes. The digeneans are restriced to habitats where its hosts are present, and a cycle relating larval hosts to adult hosts thus becomes feasible. (Baer, 1951). However, in the Crouch mixed cockle populations all three trematodes can occur in both cockles, although there may be a marked preference for a single host.

Ecological factors can play an important part in influencing which hosts are infected but in general, C. edule the typically littoral cockle is more highly infected by larval Digenea than C. glaucum occuring in marine pools. Also other symbionts such as Trichodina sp. Paravortex cardii, Pinnotheres pisum and Hermanella rostratus have not been discovered at all in lagoon habitats. The lowering of salinity, the change of ion balances, large temperature and oxygen fluctuations usually associated with the lagoon environment may preclude these Cerastoderma symbionts.

Larval trematodes have been shown to be extremely host specific in selection of the molluscan host, (Kendall, 1950; Wright, 1960; James, 1968; 1969). Of the four larval Digenea found in the Cerastoderma from the mixed cockle populations two, Cercaria B. haimeana and the metacercaria of M. minutus showed a marked difference of incidence in the two cockles.

The bucephalid is found very rarely in C. glaucum (as it is to C. edule). The infection miracidia may not be attracted to C. glaucum, or the host defensive mechanisms might normally destroy the miracidium.

It has been shown by Bowers (1969) that only spent C. edule are infected by this parasite. It has been suggested here that the weakening of spawning or some associated factor, allows penetration by the infective miracidium. In two successive spawning seasons it has been shown that C. glaucum from the Crouch mixed cockle population, spawns seven weeks after C. edule, in mid-July (see section VI). It is feasible that the definitive host migrates out of the estuary during the summer, or that the free-living miracidia cannot tolerate the higher water temperatures or salinities which occur in mid-July. Until more is known of the tolerance and behaviour of the miracidium of this trematode, no conclusions can be drawn as to whether this recorded specificity has an ecological or physiological basis.

The gymnophallid M. minutus was entirely absent from all C. glaucum examined, but invariably present in C. edule. Specificity considering this metacercaria might appear to have a truely physiological basis. However, its recorded presence as Lecithodendrium somateriae in another lamellibranch, Venerupis decussata (L.) by Jameson (1902) is confusing. If this parasite occurs in two bivalves from two separate families its absence from C. glaucum a very close relative of C. edule, is unlikely to be due to difference in physiology of the cockle hosts. This would tend to support the theory of exclusion from C. glaucum because of the absence of the required ecological niche beneath the hinge of C. glaucum. Alternatively, there have been no further records of M. minutus in V. decussata after Jameson, hence his equating of the hinge parasite of C. edule with the cysts found in the siphonal muscles of V. decussata, may have been in error. If so, it seems likely that as the infective cercariae induce a tissue reaction in C. edule which results in host formed cysts, the absence in C. glaucum

could be due to an efficient tissue defence mechanism, which eliminates the infective cercariae. Thus the absence of this parasite from C. glaucum could well have a physiological basis.

Discussing digenean life cycles, Bowers (1965) considers that the first parasitic stage is more host specific than the metacercariae in a second intermediate larval host. In general, this is probably true, but some families of the Digenea may exhibit greater degrees of specificity than others. Thus James (1968) records Cercaria (Metacercaria) C. (Crewe, 1951) between the mantle and the shell of Tatella vulgata L. but not in the close relative T. intermedia or T. aspera. This Gymnophallid is regarded by James (1968), to probably belong to the genus Meiogymnophallus (Ching, 1965). The presence at near 100% incidence of another species of this genus M. minutus in C. edule, and its complete absence from C. glaucum may indicate that the second larval stage at least of this Gymnophallid of the genus Meiogymnophallus is very specific indeed in its selection of hosts.

On the other hand, specificity at the level of first intermediate host may not be exclusive to a single species. Thus, although Bowers (1965) records six first stage larval trematodes in single species hosts from Llanrhidian Sands, South Wales, these six parasites have been recorded in the literature from one (two cercarial types), two, four, six and even nine separate lamellibranch hosts. For example, Cercaria dichotoma, recorded by Bowers only in C. edule has also been recorded in three Tellinids: Macoma balthica (L.) - Pelseneer (1906): T. Tenius (da Costa) - Miller, (1926): and Scrobicularia plana (da Costa) - White (1970). Thus on the Essex coast the incidence of this cercaria in S. plana, (exceptionally at 4% in certain populations of the host) is generally at 0.23% in 2,610 examined (White, 1970). This is very similar to that incidence recorded

here in C. edule. In different parts of the geographical range of the parasite, the host species can vary in importance depending upon local conditions of host abundance, susceptibility to infection, etc. In general, it is true to say that larval Digenea do exhibit a degree of phylogenetic lamellibranch host specificity, as typified by the trematode parasites present in the two closely related Cerastoderma examined here, but ecological factors have also been shown to be very important in regulating host availability. Knowledge of the digenean fauna of the two cockles may be useful in suggesting the evolutionary sequence of the speciation process within the Cerastoderma. The classical approach of divergence isolation and later sympatric re-association (Mayr, 1957) seems to be true when considering the Crouch mixed cockle population. Divergence in habitat preference has resulted in ecological isolation, with one form inhabiting stagnant lagoons and the other occurring inter-tidally, (Boyden, 1969; Russell, 1969). With later convergence and existence in the same environment the genetic constitution of each stock has been maintained. Cameron (1964), in an analysis of host-parasite associations concludes that the more highly specialised the host (in an evolutionary sense), the more specialised are its parasites and the more restricted its parasitic fauna. C. glaucum has a smaller incidence of trematode infection than C. edule both in lagoons and in the mixed Cerastoderma populations of the Crouch and Roach estuaries. This may suggest that C. glaucum separated from an edule stock and evolved to colonise the specialised habitat of stagnant, saline lagoons. During this period of time C. glaucum physiologically diverged from C. edule, such that upon recolonisation of a common habitat by both forms, a difference in the symbiotic fauna could then be detected. Thus the abundance of symbionts in these two members of the Cerastoderma may be regarded as evidence suggesting a separation of C. glaucum from an ancestral edule type stock.

REFERENCES

ATKINS, D., 1934. Two parasites of the Common Cockle, Cardium edule, a rhabdocoel, Paravortex cardii (Hallez) and a copepod Parenthessius rostrastus (Canu). J. mar. biol. Ass. U.K., Vol. 19, pp. 669-76.

BAER, J.G., 1951. Ecology of Animal Parasites. Univ. of Illinois Press, Urbana.

BOWERS, E.A., 1965. Studies on some parasites of sea-birds and molluscs. Ph.D. Thesis, Swansea, Wales.

BOWERS, E.A., 1969. Cercaria bucephalopsis haimeana (Lacaze - Duthiers, 1854)(Digenea: Bucephalidae) in the cockle, Cardium edule L. in South Wales. J. nat. Hist., Vol. 3, pp. 409-422.

BOWERS, E.A. & JAMES, B.L., 1967. Studies on the morphology, ecology and life cycle of Meiogymnophallus minutus (Jobbold, 1859) nov. comb. (Trematoda: Gymnophallidae). Parasitology, Vol. 57, pp. 281-300.

BOYDEN, C.R., 1969. Ecology of the cockle Cardium glaucum Bruguière. Essex. Nat. Vol. 32, part 3, pp. 223-226.

CAMERON, T.W.M., 1964. Host specificity and the Evolution of Helminthic Parasites. Advances in Parasit. Vol. 2, pp. 1-33.

CANU, E., 1891. 'Les Copepods marins du Boulonnais' V Les semi-parasites Bull. Sci. de la France et de la Belg., Tome XXIII, pp. 467-487.

CHENG, T.C., 1967. 'Advances in Marine Biology' Ed. F.S. Russell. Vol. 5, Marine molluscs as hosts for symbioses. Academic Press, London and New York.

CHRENKO, F.A., 1934. A list of Parasitic Rhadocoela (Turbellaria) of Plymouth. Parasitology, Vol. 26, pp. 114-116.

CHING, H.L., 1965. Life cycle of Lacunouermis conspicus n. gen., n. sp. and Meiogymnophallus multigemmulus n. gen., n. sp. (Gymnophallidae: Trematoda) from Macoma inconspicua and Diving Ducks from Vancova, Canada. Proc. helmun Soc. Wash., Vol. 32, pp. 53-63.

COLE, H.A., 1938. On some larval trematode parasites of the mussel (Mytilus edulis) and the cockle (Cardium edule) Part II. A new larval Gymnophallus (Cercaria cambrensis sp. nov.) from the cockle. Parasitology, Vol. 30, pp. 40-43.

COLE, H.A., 1956. Benthos and shellfish of commerce. In Sea Fisheries: their investigations in the U.K. Vol. 207-25, pp. 171-172. (Ed. M. Graham). Edward Arnold (Publishers) Ltd.

DAWES, B., 1946. The trematoda. Cambridge Univ. Press.

DELPHY, J., 1938. Etudes de morphologie et de physiologie sur la fauna d'Arachon. Bull. Soc. Sci. Arachon. Vol. 35, pp. 49-75.

FENCHEL, T., 1965. Ciliates from Scandinavian molluscs. Ophelia, Vol. 2, (1), pp. 71-174.

FIGUEIREDO, S., VILELA, H., & PENEDA, C., 1964. Recherche sur le parasitisme des mollusques bivalves de la cote portugaise. Conseil Inter. pour l'Explor. de la Mer commite des Mollusques et Crustaces. No. 53, pp. 1-3.

FRASER, J.H., 1932. Occurrence of the cyclopoid Herrmanella rostrata (Canu) in Cardium edule. Nature Vol. 130, p. 279.

FREEMAN, R.F.H., 1957, Paravortex scrobicularlae (Graff) in Great Britain. Nature, Vol. 180, p. 1213.

HALLEZ, P., 1909. Biologie, organisation, histologie et embryiologie d'un Rhabdocoel parasite du Cardium edule L. Paravortex cardii n. sp. Arch. Zool. Exper. et Gen. IV, ser. 9, pp. 429-544.

HANCOCK, D.A., & URQUHART, A.E., 1965. The determination of natural mortality and its causes in an exploited population of cockles. (Cardium edule L.) Fish. Invest. Lond. ser. II 24(2), pp. 8-10 (pp. 40)

HARGIS, W.J., 1957. The host specificity of monogenetic trematodes. Expt. Para. Vol. 6, pp. 610-625.

HEYNEMANN, D., 1960. On the origin of complex life cycles in digenetic trematodes. Sobretiro del Libro Homenaje al Dr. Eduardo Cabellero Cabellero, Mexico.

HOLLOWAY, E.D., 1949. A preliminary report on the Plymouth marine and brackish-water Rotifera. J. mar. biol. Ass. U.K., Vol. 28, pp. 239-253.

HOPKINS, S.H., 1954. The American species of trematode confused with Bucephalus (Bucephalopsis) haimeanus. Parasitology, Vol. 44, pp. 353-370.

HØPNER-PETERSEN, G., 1956. Notes on the growth and biology of the different Cardium species in the Danish brackish water areas. Medd. Dan. Fisk-og Havunders, Ny. serie, Vol. 2, no. 22, pp. 1-31.

HUET, M., 1883. Note sur un parasite noveau du Cardium edule. Bull. Soc. Linn. Normandie, Vol. 2, ser. 4, pp. 149-152.

HUTTON, R.F., 1952. Studies on the parasites of Cardium edule L.: Cercaria fulbrighti n. sp. Gymnophallus larvae with a forked tail. J. mar. biol. Ass. U.K., Vol. 31, pp. 317-326.

JAMES, B.L., 1964. The life cycle of Paratrema homoeotecnum sp. nov. (Trematoda: Digenea) and a review of the family Gymnophallidae Morozov, 1955. Parasitology, Vol. 44, pp. 1-41.

JAMES, B.L., 1968. The occurrence of larval Digenea in ten species of intertidal prosobranch molluscs in Cardigan Bay. J. nat. Hist., Vol. 2, pp. 329-343.

JAMES, B.L., 1969. The Digenea of the Intertidal Prosobranch Littorina saxatilis (Olivi). Sonderdruss. Zool. Systematik Evolutionsforschung Bd., Vol. 7, pp. 273-316.

JAMES, B.L. & BOWERS, E.A., 1967. Studies on the morphology, ecology and life cycle of Meiogymnophallus minutus (Cobbold, 1859). Camb. nov. (Trematoda: Gymnophallidae). Parasitology, Vol. 57, pp. 281-300.

JAMESON, H.L., 1902. On the origin of pearls. Proc. Zool. Soc. Lond. Vol. 1(2), pp. 140-166.

JAMESON, H.L. & NICOLL, W., 1913. On some parasites of the scotex duck (Oedemiae nigra) and their relation to the pearl-inducing trematode in the edible mussel (Mytilus edulis). Proc. Zool. Soc. Lond. Vol. 12, pp. 53-63.

JOHNSTON, J., 1904. Internal parasites and diseased conditions of fishes Rep. Lanc. Sea Fish. Sci. Invest. for 1904, pp. 98-120, 151-191.

JOHNSTON, J., 1921. Diseases and parasites of fishes. Rep. Lanc. Sea Fish. Laboratory, Vol. XXIX-XXXI, pp. 233-235.

KENDALL, S.B., 1964. Some factors influencing the development and behaviour of trematodes in their molluscan hosts. In 'Host Parasite relationships in Invertebrate hosts' 2nd Symposium of the British Society for Parasitology. Ed. Angela E.R. Taylor, pp. 51-73. Oxford Blackwell Scientific Publications.

LACAZE-DUTHIERS, F.J.H. de., 1854. Memoire sur le Bucephale Haime (Bucephalus haimeanus) helminth parasite de huitres et des Bucardes. Annals des Sci. nat. (Zool.)(Ser. 4) Vol. 1, pp. 249-302.

LA RUE, G.R., 1957. The Classification of the digenetic trematodes. A review and a new system. Exp. Parasitol. Vol. 6, pp. 306-349.

LEBOUR, M.V., 1904. A preliminary note on a trematode parasite in Cardium edule. Northumberland Sea Fish. Report 1904. pp. 82-84.

LEBOUR, M.V., 1905. Notes on Northumberland trematodes. Rep. Scient. Invest. Northumb. Sea Fish. Comm. Dec. 1903, pp. 100-105.

LEBOUR, M.V., 1907. Larval trematodes of the Northumberland Coast. No. 1. Trans. Nat. Hist. Soc. Northumb. N.S., Vol. 1, pp. 437-454.

LEBOUR, M.V., 1908. Trematodes of the Northumberland Coast, No. 2. Trans. Nat. Hist. Soc. Northumb. N.S., Vol. 2, pp. 28-45.

LEBOUR, M.V., 1911. A review of the British Marine Cercariae. Parasitology Vol. 4, pp. 416-456.

LEIGH-SHARPE, W.H., 1933. A second list of parasitic Copepoda of Plymouth with a description of three new species. Parasitology, Vol. 25, pp. 113-118.

LINTON, E., 1910. On a new rhabdocoel commensal with Modiolus plicatulus J. exp. Zool. Vol. 9, pp. 371-386.

LLEWELLYN, J., 1965. The evolution of parasitic platyhelminthes. In 'Evolution of Parasites'. Ed. Anela E.R. Taylor, pp. 47-78. Oxford Blackwell Scientific Publications.

MADDOX, R.L., 1867. Some remarks on the parasites found in the nerves, etc. of the common haddock. Jour. Micros. Scr. Vol. 7, N.S., p. 87.

MAYR, E., 1957. Species concepts and definitions. In E. Mayr, ed, 'The species problem'. Amer. Assoc. Adv. Sci. Publ. No. 50, pp. 1-22.

MILLER, H.M., Jr., 1926. Comparative studies on furcocercous cercariae. Illinois Biol. Monogr. Vol. 10 (3), pp. 265-370.

MOULINIE, J.J., 1856. De la reproduction chez les trematodes endoparasites Mem. Inst. Nat. Genevois Vol. 3, pp. 7-278.

NICOLL, H.W., 1906. Notes on the Trematode Parasites of the cockle, (Cardium edule) and the mussell (Mytilus edulis). Ann. Mag. Nat. Hist. Ser. 7, Vol. 17, pp. 148-155.

NICOLL, W.W., 1914. Trematode parasites of fishes from the English Channel J. mar. biol. Ass. U.K., Vol. 10, pp. 466-505.

PELSENEER, P., 1906. Trématodes parasites de mollusques marins. Bull. Sci. de la France et Belge. Ser. 5, Vol. 9, p. 161-186.

PETERSON, R., MOUNTFORT, R., & HOLLOM, P.A.D., 1965. A field guide to the birds of Britain and Europe. Collins, London, pp. 58-59, p. 118.

PICKFORD, G.E., & McCONNAUGHEY, B.H., 1949. The Octopus bimaculatus problem: a study in sibling species. Bull. Bingham Ocean. Coll., Peabody Mus. Nat. Hist. Yale Univ. Vol. 12, pp. 1-66.

RAABE, J. & RAABE, Z., 1959. Urceolariidae of molluscs of the Baltic Sea. Acta. Parasit. polon., Vol. 7, pp. 453-465.

RAABE, Z., 1963. Systematics of the family Urceolariidae Dujardin 1841. Acta. Protozool., Vol. 1, pp. 121-138.

REES, F.G., 1939. Cercaria striata Lebour from Cardium edule and Tellina tenuis Parasitology, Vol. 31 (4), pp. 458-463.

REYNOLDSON, T.B., 1948. British species of Polycelis (Platyhelminthes). Nature. Vol. 162, p. 620.

RUSSELL, F.J.C., 1969. Studies on the ecology, distribution and morphology of the cockles Cardium edule L. and C. glaucum Bruguière. Ph.D. Thesis, London.

SCOTT, T., 1892. On some new and rare crustacea from the Firth of Forth. Ann. Mag. Nat. Hist. Vol. X (number 57), pp. 201-6.

SEED, R., 1969. The incidence of the Pea Crab Pinnotheres pisum in the two types of Mytilus (Mollusca: Bivalvia) from Padstow, south-west England. J. Zool., Lond. Vol. 158, pp. 413-420.

SPARHN, C.E.W., 1933. Trematoda. In Grimpe u. Wagler, Die Tierwelt der Nord-u Ostsee, Lief. 24, Tiel, 4c. pp. 1-60 Leipzig.

STOCK, J.H., 1968. Copepoda endoparasitic of tropical holothurians. Bull. Zoologish Mus. Univ. Amsterdam Vol. 1, No. 9, pp. 89-105.

STUNKARD, H.W. & UZMANN, J.R., 1958. Studies on digenetic trematodes of the genera Gymnophallus and Parvatrema. Biol. Bull. mar. biol. Lab., Woods Hole, Vol. 115, pp. 276-302.

TEBBLE, N., 1966. British Bivalve Seashells. Trustees of the British Museum (Natural History) London.

THOMPSON, I.C., 1893. Revised Report on the Copepoda of Liverpool Bay. Proc. & Trans. Liverpool Biol. Soc. Vol. VII, pp. 175-230.

TURK, S.M., 1964. The British species of Cardium. The Conchologists Newsletter, Conchological Society of Gt. Brit. and North. Ireland, no. 10, pp. 58-62.

WHEELER, A., 1969. The Fishes of the British Isles and North-west Europe. London, Macmillan.

WHITE, I.C., 1970. Aspects of the ecology and physiology of the digenetic trematode Proctoeces subtenuis (Linton). Ph.D. Thesis, London

WILLIAMSON, H.C., 1911. Notes on the eggs of the Angler etc. 28th Ann. Rep. Fish. Board, Scotland.

WRIGHT, C.A., 1960. Relationships between trematodes and molluscs. Ann. trop. Med. Parasit. Vol. 54, pp. 1-7.

YAMAGUTI, S., 1958. The digenetic trematodes of vertebrates. Systema Helminthum, Vol. 1. pp. 1575, London & New York: Inter-Science Publications.

SECTION - VIII

SECTION VIII

THE BEHAVIOUR, SURVIVAL AND RESPIRATION OF THE COCKLES CERASTODERMA EDULE(L) AND CERASTODERMA GLAUCUM (POIRET) IN AIR.

Introduction.

The ecology of the common, commercial cockle Cerastoderma edule(L.) is now well understood (Orton, 1926; Thamdrup, 1935; Kreger, 1940; Kristensen, 1956). Predominantly an inter-tidal animal, C. edule can occur sub-littorally, in contrast to the less well-known Cerastoderma glaucum (Poiret) which is typically found in stagnant marine lagoons, (Boyden, 1969; Russell, 1969), but can occasionally occur intertidally.

The existance of a mixed cockle population in the estuary of the River Crouch, Essex, provided an opportunity to compare some aspects of the behaviour and physiology of these animals, under circumstances where differences could not be attributable to differences in the environment.

This paper reports the results of investigations into the behaviour and survival in air, and the respiration, of these two lamellibranchs.

Material & Methods

The cockles used in this study were collected from the mixed cockle population of the Crouch estuary at Fullbridge 'ferry', Essex. They were separated into the two types, - C. edule and C. glaucum, using the shell morphological criteria of Wegner-Peterson (1958):- (see also Tebble, 1966).

A vertical shore transect was conducted of the mixed cockle population. Samples ($0.1m^2$) were taken at metre intervals from low-water mark. The substrate to a depth of about 15 cms. was sieved in a 5mm. mesh sieve, and the cockles counted and averaged.

For the experimental work, cockles were collected between low water springs and low water neaps, scrubbed clean of algae and silt and transferred to polythene tanks in a constant temperature room at 15°C. Here they were maintained in a large volume of frequently changed, filtered, aerated sea water of 33-34.5‰ salinity.

Desiccation experiments were conducted within a 10 L. aquarium covered by a ground glass lid. Activated silica gel. and anhydrous calcium chloride were placed in glass chromatography troughs on either side of the aquarium base, and these maintained the tank relative humidity (R.H.) between 0 and 40%. Movement of the chamber air, to equalise the overall humidity, was achieved by a central stirrer -(swept-plate vortex generator of Dryer, 1962). To relate water loss to mortality, cockles were wedged open to remove all the mantle cavity water, and thus loss of water only took place from the body tissues. The water loss from the shell during these experiments was substracted from the total loss.

Temperature tolerance in air was determined by placing cockles upright in damp, fine gravel within aquaria. The tank sides and roof were covered by wet filter papers. Groups of 20 similar sized cockles

were placed in substrate at six different temperatures between 10°C and 35°C. They were examined regularly to determine condition and were considered dead when there was no contraction response of the adductor muscles to leverage separating the valves. Later experiments conducted using cockles with valves clamped shut by bosshead clamps were executed in a comparable manner. Similarly an airtight chromatography tank with damp substrate and filter papers, was used for determining the tolerances of the cockles to anaerobic conditions. Oxygen free nitrogen was humidified by bubbled through water before flushing through the tank. The tank was flushed twice daily with nitrogen, and the air-tight lid sealed with vaseline.

An expression of the meta olism in air and water was obtained by visual observation of rate of heart-beat. A small hole was drilled through the shell below the ligament and directly above the pericardium using a water cooled bit. The cockles were transferred to small bowls half-filled with fine gravel, and allowed to adjust for 2-3 days to recover from operative shock; only those individuals exhibiting normal extension of the siphons were used. The pulsations of the ventricle were observed by binocular microscope through the pericardium. The temperature of water and air was maintained at 15°C. (± 1°C), and mechanical disturbances were reduced to a minimum. Tidal conditions were simulated by gentle siphoning of water into and out of the bowls.

The behaviour of cockles was also determined in air and water. Experimental animals were inclined at about 45° and the lower valve was cemented to a perspex block, which in turn was clamped to the bottom of an aquarium. A cotton thread was attached to the upper valve of the cockle, and to an isotomic spring level, the pointer of which scribed on a smoked drum kymograph. (see fig. 1). Water was added to the quarium and the

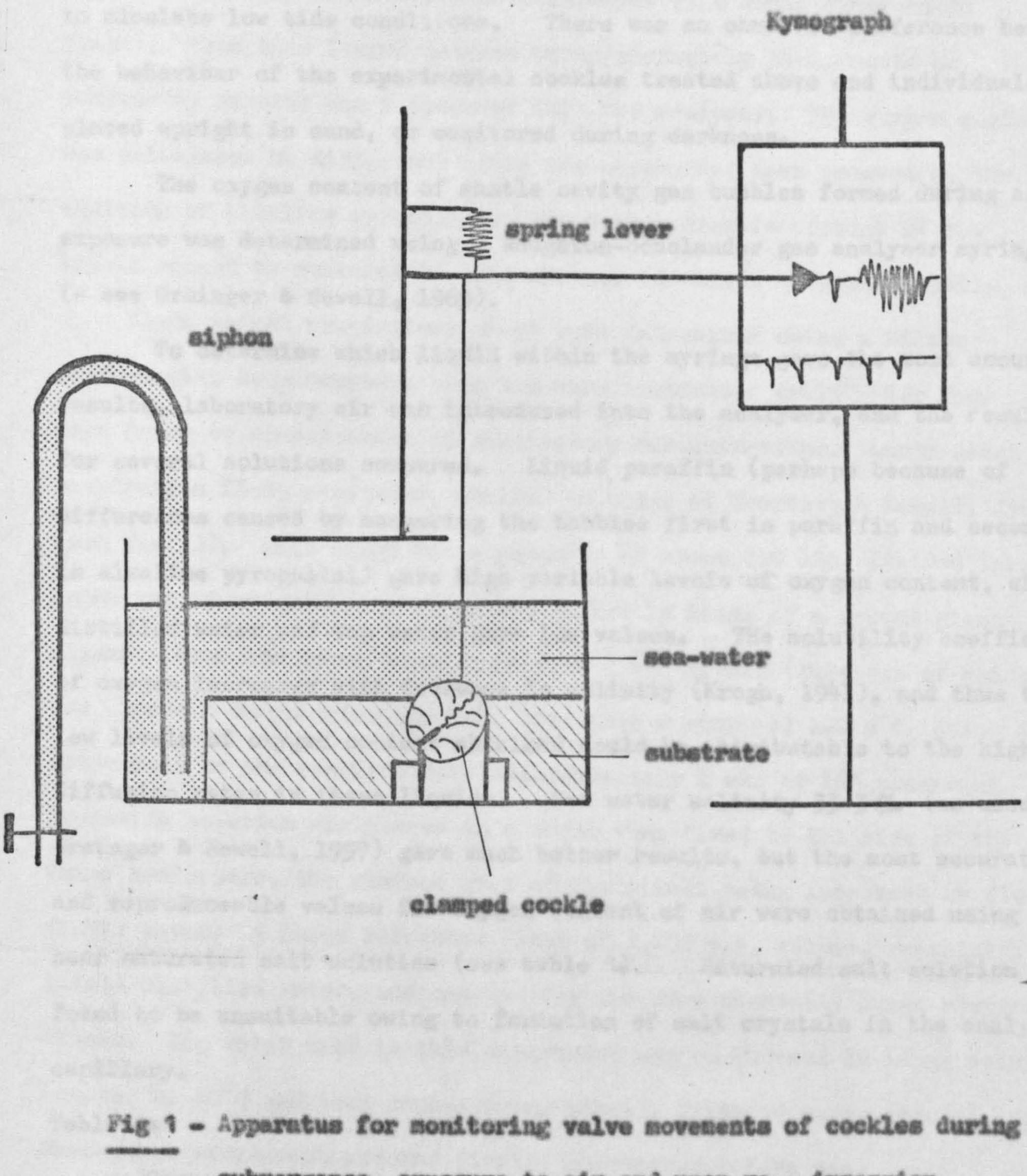


Fig 1 - Apparatus for monitoring valve movements of cockles during submergence, exposure to air and upon re - immersion.

experimental cockles left overnight to adjust to the conditions, before commencement of the experiment. A siphon facilitated the removal of water to simulate low tide conditions. There was no observed difference between the behaviour of the experimental cockles treated above and individuals placed upright in sand, or monitored during darkness.

The oxygen content of mantle cavity gas bubbles formed during aerial exposure was determined using a Roughton-Scholander gas analyser syringe (- see Grainger & Newell, 1965).

To determine which liquid within the syringe gave the most accurate results, laboratory air was introduced into the analyser, and the results for several solutions compared. Liquid paraffin (perhaps because of differences caused by measuring the bubbles first in paraffin and secondly in alkaline pyrogallal) gave high variable levels of oxygen content, whereas distilled water and tap water gave low values. The solubility coefficient of oxygen increases with decrease in salinity (Krogh, 1941), and thus the low levels of oxygen content obtained could be attributable to the higher diffusion rates in these liquids. Sea water salinity 33-34‰ (as used by Grainger & Newell, 1957) gave much better results, but the most accurate and reproduceable values for oxygen content of air were obtained using near saturated salt solution (see table 1a. Saturated salt solution were found to be unsuitable owing to formation of salt crystals in the analyser capillary.

Table 1a.

Comparison of percentage oxygen content of laboratory air, using sea water (33-34‰) and near saturated salt solution.

	Solution	
	Sea water	Near saturated sodium Chloride solution
Number of determinations	25	25
Range of values of percentage oxygen content	19.38 - 21.32	20.12 - 21.30
Mean value of percentage oxygen content	20.19	20.86

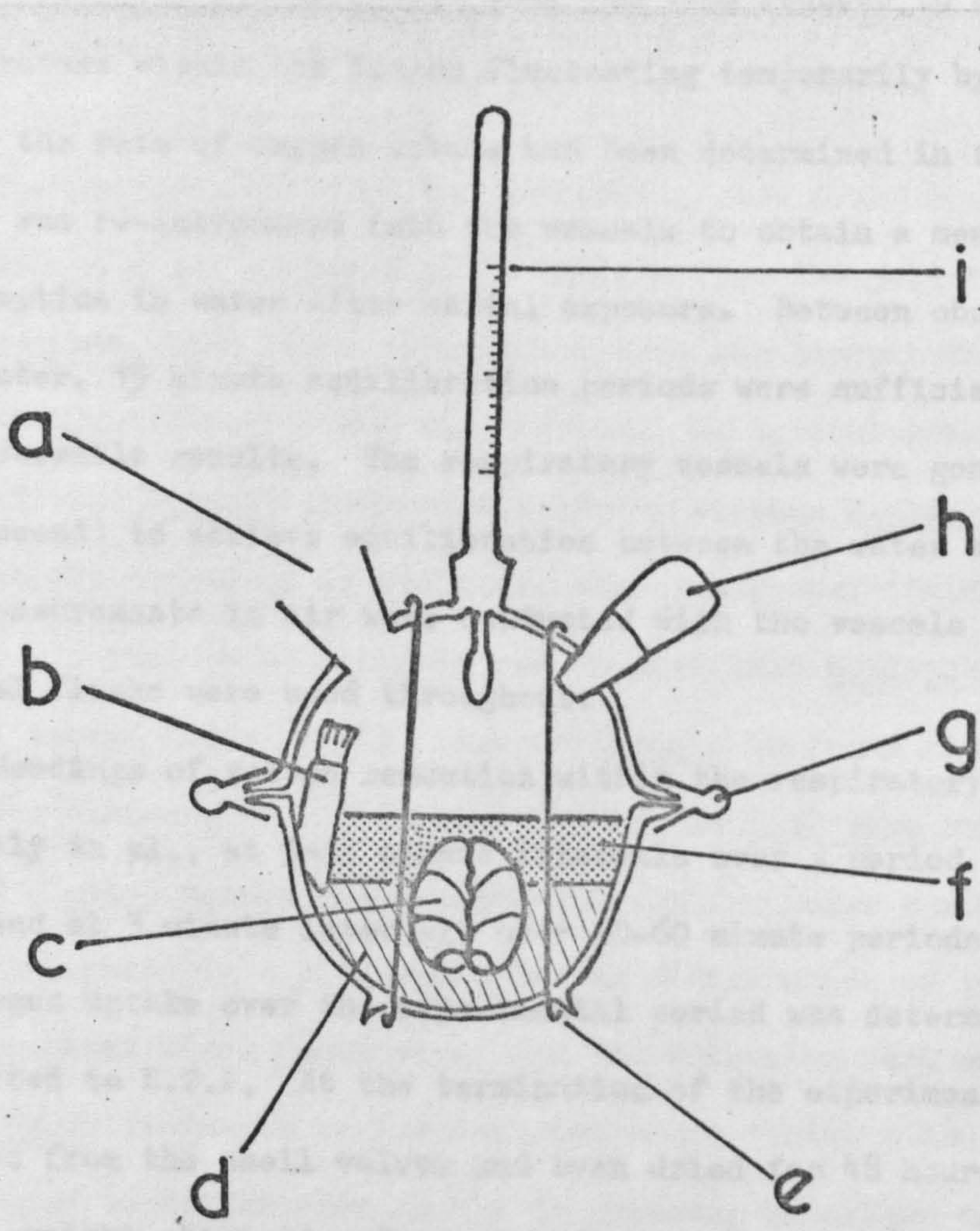
(Percentage oxygen content of air = 20.95 (Krogh, 1941)

Cockles were immersed in concentrated saline after a period of exposure, and the bubbles released captured in a small close-ended funnel. From this funnel bubbles of approximately 38µl. could be removed by pipette and introduced into the analyser. The oxygen content was calculated by difference after the oxygen had been removed by the addition of alkaline pyrogallal. The carbon dioxide content of the bubble cannot be measured in this system. (Grainger & Newell, 1965).

Whole animal respiratory rates were determined using a Gilson Differential Respirometer. Cockles were acclimated to 15°C for four days prior to commencement of respiratory determinations. Large glass respiration flaks were used, similar to those of Courtney & Newell, 1965, (see Fig. 2). Each flask has a capacity of about 110 mls. divided into upper and lower chambers, which are joined by means of a ground glass flange. From the upper hemisphere were 2 B_{10} joints (into one of which was placed a thermometer and into the other a stopper) and a C_{4} joint for attachment to the respirometer. Approximately 1 ml. of 18% potassium hydroxide solution was placed in a small tube fixed to the side of the lower hemisphere, the surface area of the alkali being increased by fluted filter paper. A large reference flask of 1,000 c.c. volume, containing a little distilled water, compensated for the nine unusually large respiratory flasks. The water used in this experiment was pasteurised in large volume (heated to 60°C and then cooled three times), filtered under reduced pressure through an oxoid membrane and finally re-aerated before use.

Sterile sand to a depth of 2-3 cms. was placed in the lower hemisphere, and the experimental cockles were left overnight buried in the substrate within these vessels. The flasks containing 10 mls. of water were attached to the respirometer and 45 minutes allowed for equilibration. After the

Fig 2 - Jointed respiratory vessel (volume 100 mls.) used in whole animal respiration study



-Key

a = C_{14} joint to the Gilson Respirometer

b = side tube containing potassium hydroxide

c = experimental cockle

d = sterile sand

e = bands clamping the two glass hemispheres

f = sea - water

g = clamps at the ground glass junction of the hemispheres

h = B_{10} stopper

i = thermometer

aquatic rate of oxygen consumption had been determined, the original 10 mls. of flask water was removed by syringe through one of the B_{10} joints. Disturbance and equilibration time was thus reduced to a minimum, the temperature within the flasks fluctuating temporarily by a maximum of 0.5°C. After the rate of oxygen uptake had been determined in the air, 10 mls. of water was re-introduced into the vessels to obtain a measure of oxygen consumption in water after aerial exposure. Between observations in air and water, 15 minute equilibration periods were sufficient to obtain reproduceable results. The respiratory vessels were gently shaken (once per second) to achieve equilibration between the water and flask air, whilst the measurements in air were conducted with the vessels stationary. Two control flasks were used throughout.

Readings of volume reduction within the respiratory vessels were made directly in µl., at 5-15 minute intervals over a period of 60-90 minutes in air, and at 3 minute intervals over 30-60 minute periods in water. The rate of oxygen uptake over the experimental period was determined in µl/hr and converted to N.T.P. At the termination of the experiment the tissues were removed from the shell valves and oven dried for 48 hours at 100°C and dry tissue weight obtained. Oxygen uptake was then expressed as µl O_2/mg./hr. The regression lines were calculated by the method of least squares.

Results and Observations

1. Shore distribution of Cerastoderma edule(L.) and Cerastoderma glaucum (Poiret) in the Crouch estuary.

The graphed result of the transect of the mixed cockle population is shown in Fig. 3. (See Fig. 8, Section V). The pattern which emerges follows that which might be expected from the distribution of single species populations of the two cockles. In typical separate cockle populations, C.edule occurs intertidally whereas C.glaucum is found permanently submerged in stagnant, saline lagoons. (Boyden, 1969; Russell, 1969). On the Crouch shore it can be seen that C.glaucum occurs abundantly at the lowest shore levels, whereas C.edule is found at a similar density for some distance up the shore. 50% of the C.glaucum collected were found in the first 3 metres shore distance from low water spring mark.

Thus there is a difference in the distribution of the two cockles in this shore mixed population, and the following work was conducted in order to determine to what extent the shore distribution could be attributed to differences in the tolerances, behaviour and physiology of these two cockles.

Investigation of Desiccation Effects

The resistance to desiccation when exposed to air is one factor which has been shown to be important in the vertical distribution of many littoral animals (see Newell, 1964). Thus rocky shore gastropods (Broekhuysen, 1940; Micallef, 1966; Davis, 1969), barnacles (Barnes & Barnes, 1957; Grainger & Newell, 1965) have been studied from the viewpoint of water loss in relation to zonation. Differences in tolerance to water loss ould be important in explaining the observed shore distribution of C.edule and C.glaucum.

The percentage water loss from the tissues before death was slightly greater in C.edule than in C.glaucum. The latter cockle tolerated up to 33% water loss, death occurring between 33-38%, whilst six C.edule averaged 42.9 water loss, and all recovered. These values are similar to those obtained by Lent, (1969), studying Modiolus demissus, who records that the extreme limit of tolerance for this American bivalve as 36-38% water loss.

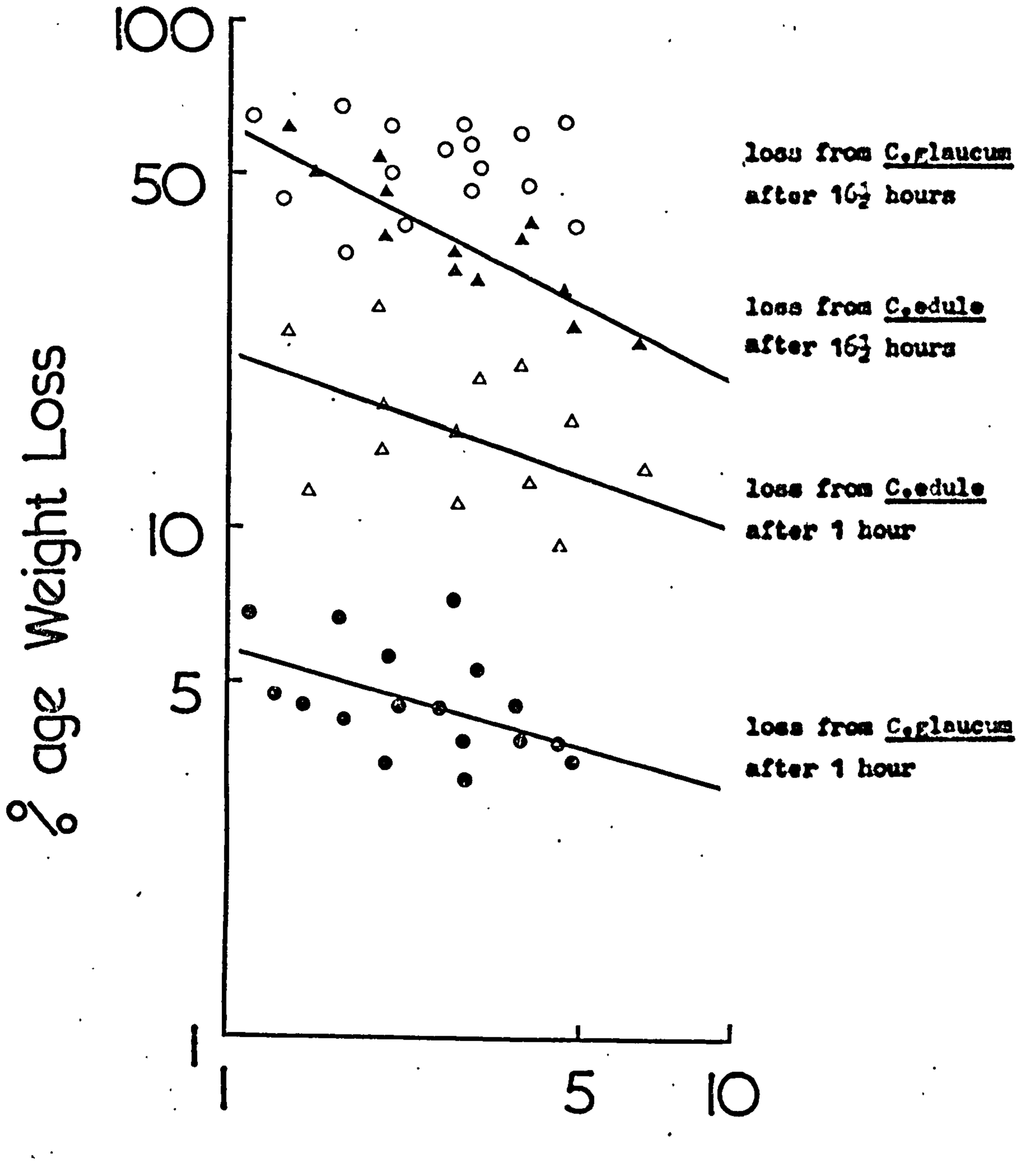
Thus C.edule can tolerate a slightly higher water loss than C.glaucum. However, on a particulate shore it is unlikely that desiccation is all that important as regards to zonation of the burrowed fauna. It has even been shown by Davis (1969) that on rocky shores, limpets seldom lose more than 10% of their body weight, ~~loss~~, while the animal in the laboratory can recover from as much as 60-65% weight loss.

A more important difference was noted in the rate of water loss from the two cockles. Individuals were weighed immediately upon removal from sea-water (i.e. containing mantle cavity water), after one hour in the desiccating chamber and again after 16½ hours. C.edule initially lost water rapidly from the mantle cavity (see Fig. 4), whereas C.glaucum did not show the same loss after one hour, but after 16½ hours had lost slightly more water than C.edule. This difference is explained by the behaviour of the cockles in air; the shell valves of C.edule immediately parting in air, whilst they remain closed in C.glaucum (see later).

Differences in thermal tolerances in air between the two cockles.

In the literature there is much information concerning the upper limit of temperature tolerances of littoral and sub-littoral species (reviewed by Orr, 1955; Gunter, 1957; Fraenkel, G. 1960 and Newell, 1970). The measurement of these lethal temperatures was conducted in water, some workers heating the water and animals relatively slowly, whilst others have warmed the animals more rapidly. ~~Moreover~~ However, it has recently been shown that

Fig 4 - Water loss calculated as percentage weight loss from cockles in a desiccating chamber. - (lines fitted by eye)



the temperature tolerance of the cockle C.edule in water, varies depending upon the volume of water used (Russell, 1969). Finally, on a temperate shore it is during periods of aerial exposure at times of low tide that extreme temperatures are likely to occur. Conditions are considerably different during aerial exposure as regards to oxygen availability and ability to eliminate excretory products. Thus the temperate tolerances of the two cockles was determined in air in a damp environment.

Graphs of percentage mortality against time have been constructed and are shown in Fig. 5. At temperatures between 10-25°C C.edule survived longer than C.glaucum, and this is also reflected in the $L.D._{50}$'s shown on table 1. Thus in experimental conditions in damp air, C.edule is better able to tolerate aerial exposure than C.glaucum. Therefore the failure of C.glaucum to colonise higher shore levels is probably related to an inability to tolerate aerial exposure and its consequent conditions.

Observation on heart beat frequency

During aerial exposure a reduction in the level of metabolism of various intertidal molluscs has been shown to occur. This has been suggested to be correlated with reduced availability of oxygen and leads to economy of available oxygen (Trueman, 1967 and Newell 1970). Thus the heart beat frequency (heartrrate) of Mytilus edulis (Schlieper, 1957; Helm & Trueman, 1967) and C.edule (Trueman, 1967) has been shown to be suppressed during aerial exposure. Kristensen (1969) comparing the heart rhythms of a sublittoral limpet Diadora nebecula and a littoral limpet Patella coerulea, from the Mediterranean, noted a slow decrease in heart rate of D.nubecula which ended in complete stopage and death, whilst in P.coerulea the heart beat frequency remained constant, but cessations of beating occurred, the pauses increasing with length of exposure.

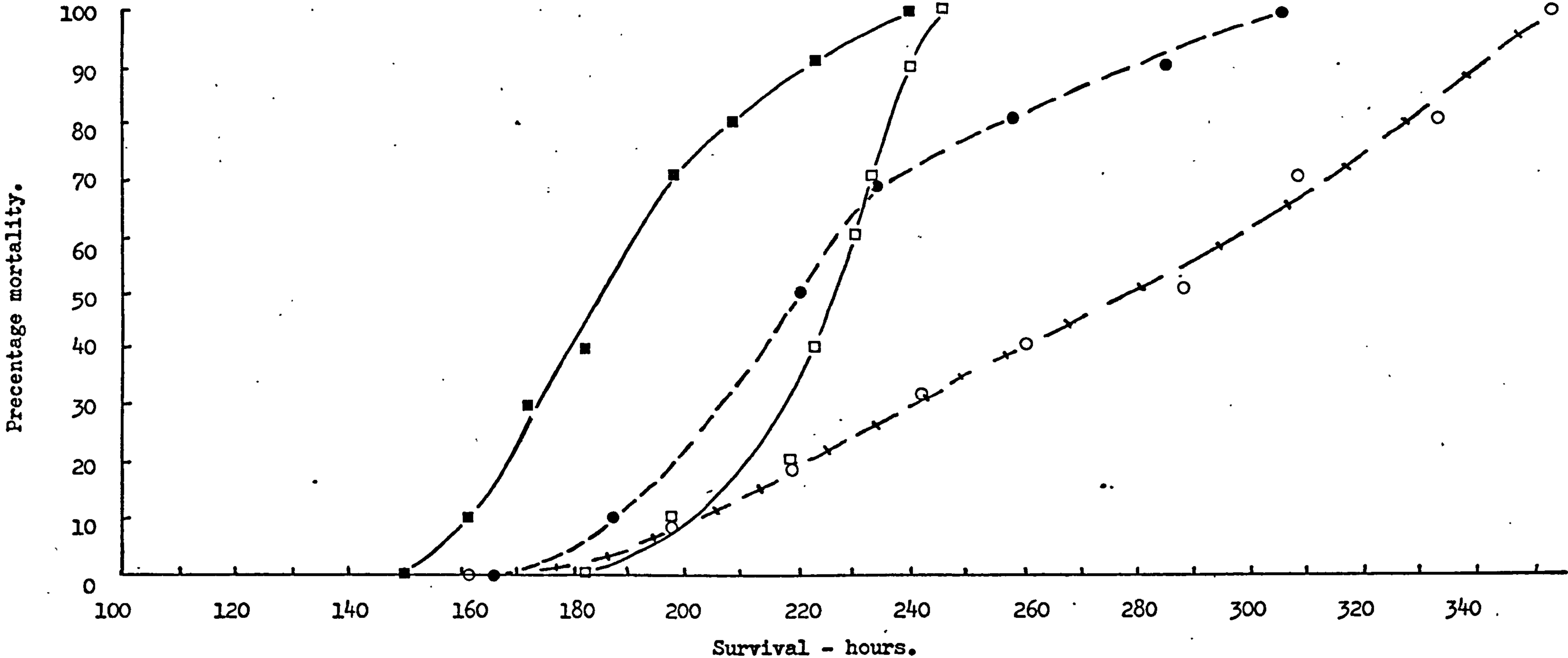


Fig 5 - Examples of two time / temperature graphs for mortality of C.edule and C.glaucum in air.

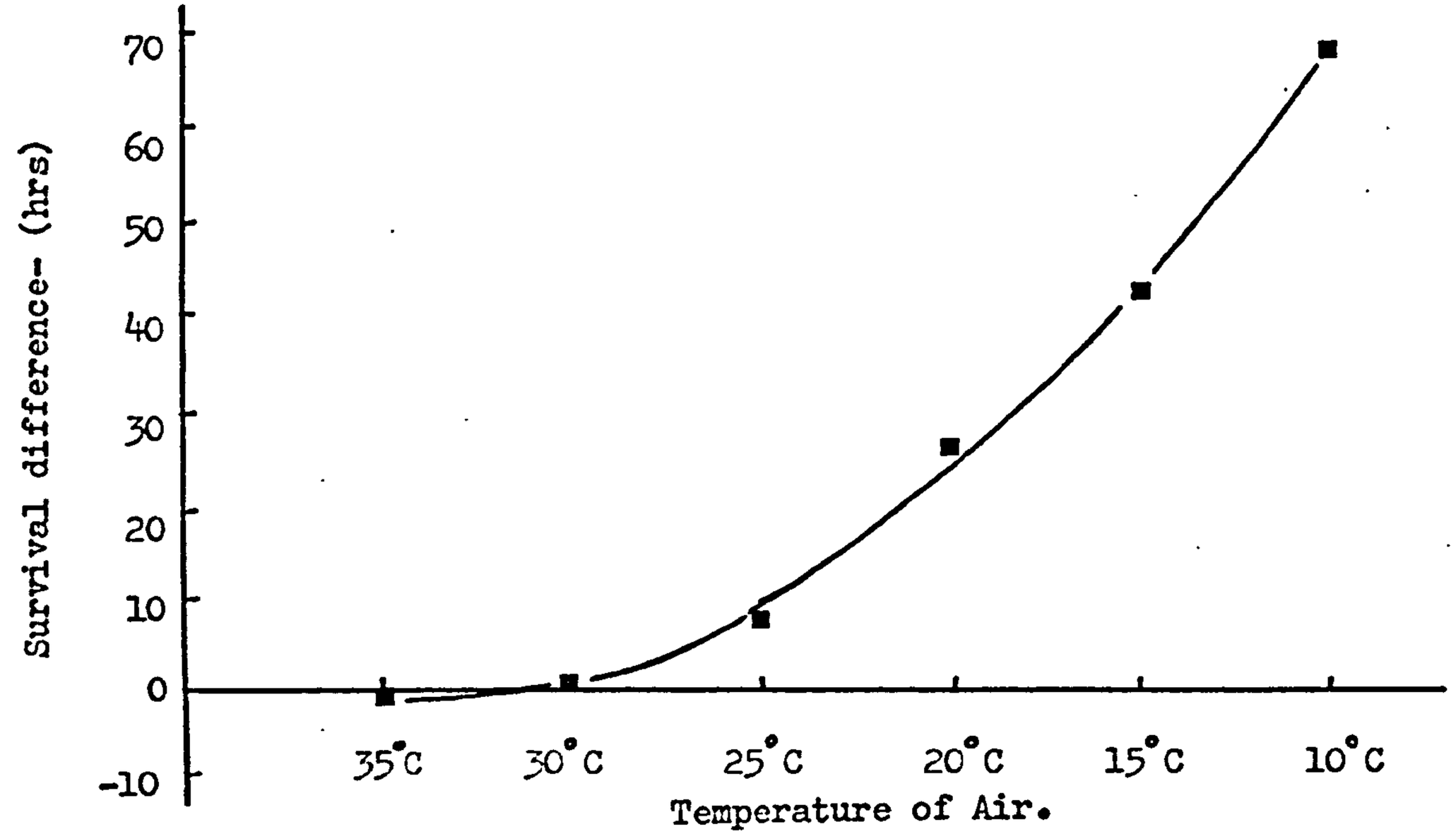
at 15 °C	at 10 °C
■——■ = C. glaucum.	●– – –● = C. glaucum.
□——□ = C. edule.	○+– –+○ = C. edule.

Table 1 - Tolerance of cockles collected from the Crouch mixed population to aerial conditions.

Length of survival at various temperatures- 50% mortality.

Species \ Temp.	35°C	30°C	25°C	20°C	15°C	10°C
C. edule	9.5 hrs.	20 hrs.	54.0 hrs	89.5 hrs.	129 hrs.	289 hrs.
C. glaucum	9.7 hrs.	19.hrs.	42.0 hrs	62.3 hrs.	86.7 hrs.	220.5 hrs.
Difference	- 0.2 hrs.	1.hr.	8 hrs.	27.2 hrs.	42.3 hrs.	68.5 hrs.

Difference between L.D.$_{50}$'s of C.edule and C.glaucum in air at various temperatures.



The observed differences in mortality during aerial exposure between C.edule and C.glaucum could reflect differences in the control of body metabolism during aerial exposure. Thus the heart beat rhythms of the two cockles have been investigated in water and in air.

Heart rate of Mytilus californianus and Acmaea limatula have been shown to vary with intertidal height, being faster at a particular temperature in the low shore animals (Segal, 1956; Dickens, 1955). The Crouch cockles C.edule and C.glaucum were collected from a single tidal level, mean low water, and compared with C.glaucum from Tidewater Lagoon, Sussex, where the cockles are permanently submerged.

The average results for six individuals of each cockle type are shown below:-

Average heart rate of cockles at 15°C prior to, during and after aerial exposure.

	(IN WATER)	(IN AIR)		(IN WATER)
Cockle type and habitat origin	Heart rate before exposure	Heart rate during exposure After 5 mins	After 3 hrs	Average of maximum ra after exposure
C.glaucum from Tidewater Lagoon	15.6	15.2	13.8	18.5
C.glaucum from River Crouch	16.1	15.0	14.5	17.5
C.edule from River Crouch	15.3	17.3	12.5	19.3

From consideration of the above there does not appear to be a fundamental difference between the heart rate of C.glaucum collected from a permanently submerged location and those cockles collected from the Crouch low shore for the general pattern of heart rhythms in the cockles, see also Fig. 6. There is a gradual small reduction of heart beat during aerial

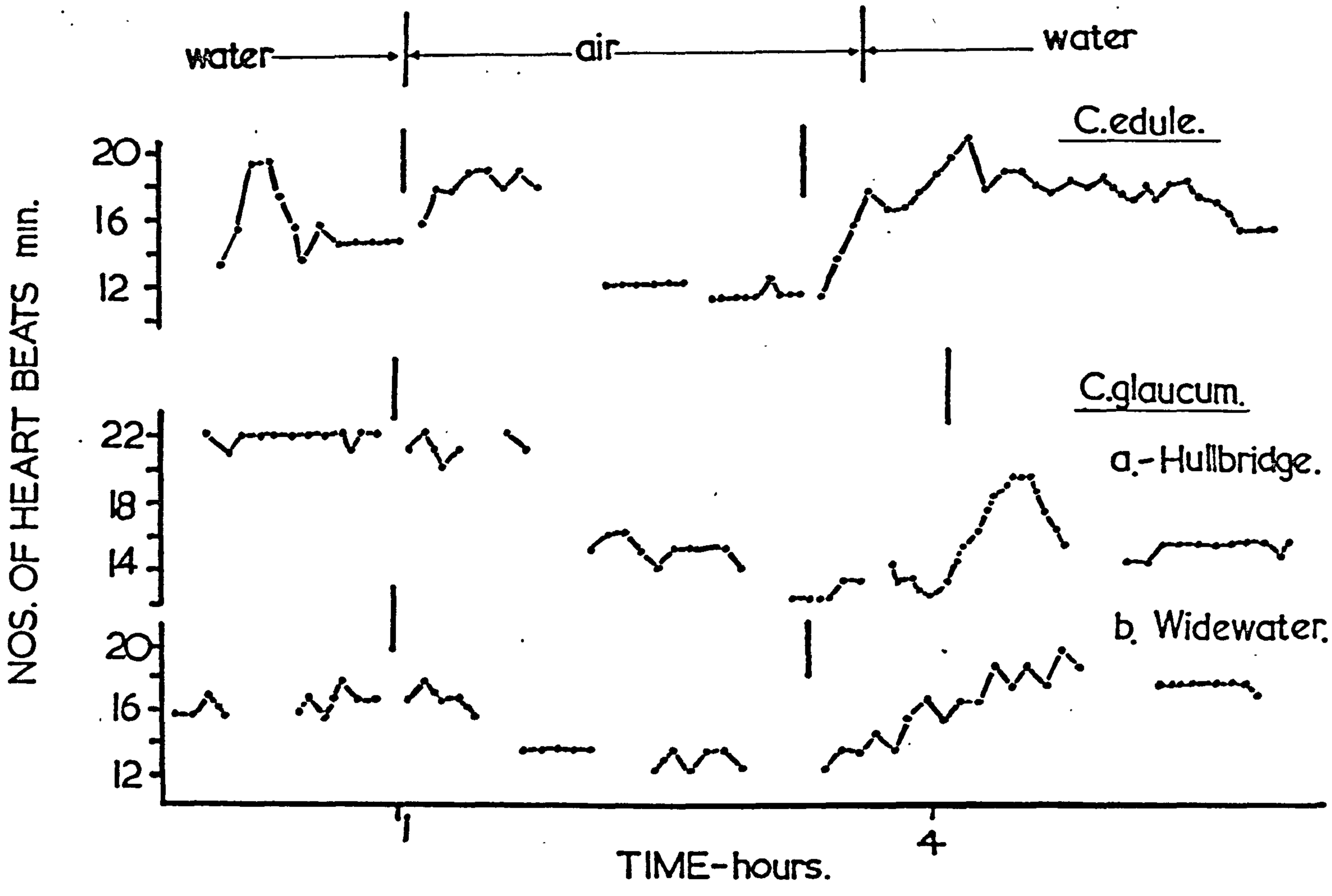


Fig - 6 HEART BEATS OF COCKLES MONITORED DURING A SIMULATED TIDAL CYCLE.

exposure in C.glaucum with a subsequent slight increase in rate after exposure. In C.edule there is initially an increase in heart beat upon exposure, then a slight bradycardia occurs; finally upon re-immersion the rate is increased. The amplitude of the beat after exposure is greatly increased in both cockles.

Trueman (1967) recognised the same general picture in heart beat of C.edule in relation to exposure. He correlated the increase in rate at the beginning of low tide conditions with increased activity of t is cockle. This activity is examined in the following section. C.glaucum does not exhibit this activity and a gradual reduction of heart beat occurs throughout the period of exposure.

The differences in survival between the two cockles in air cannot therefore be attributed to differences in metabolism as reflected by examination of the heart beat rhythms.

Investigation into the ability of the cockles to conduct aerial respiration

Observations on behaviour in air.

It was noticed during the previous experiments that there was a fundamental difference in behaviour between the two cockles in air:- C.edule tended to separate the valves upon emersion whereas C.glaucum remained tightly closed (see plates 1 and 2).

Three criteria were adopted to describe behaviour in air:

(a) Valves widely separated, gape >1 mm., mantle edges clearly visible = gaping.

(b) Valves slightly apart, gape <1 mm., mantle not exposed at shell edges = partial gaping.

(c) Valves closely apposed = closed.

Cockles were placed upright in substrate and their behaviour

Plate 1 - Showing the 'gaping' phenomenon of C. edule during aerial exposure. Note the presence of access to the mantle cavity through the contracted siphons and between the mantle edges.

Plate 2 - Photograph of C. glaucum in air. Note the absence of 'gaping' and the straight valve junction in this cockle.

Plate 1

Plate 2

noted - see table 2. Within 10 minutes the valves of C.edule separated exposing the mantle edges. After about an hour in air, (at 15°C R.H. 98%), connection between the mantle cavity and the external air became possible in many individuals through the two contracted siphons. Upon further exposure the valve gape often increases and an opening appears between the mantle fringes. With extreme exposure, the shell dries, the mantle edges become slightly withdrawn from the shell valve edges but nevertheless remain clearly visible. C.glaucum remains tightly closed throughout, and even if partial gaping occurs, the mantle edges are well withdrawn from the valve junction.

Recordings of the valve movements of C.edule and C.glaucum

In Water

Kymograph traces of valve movements in water indicated a fairly regular contraction of the adductor muscles about once every five minutes in both cockles, see Fig.7. Such behaviour has been recognised by Trueman (1967) and suggested by Jørgenson (1966) to be associated with ejection of pseudo-faeces from the mantle cavity. Such activity is certainly more common in water containing fine silt in suspension.

In Air

Upon removal of water the difference in behaviour in air becomes obvious. C.edule upon emersion, exhibits rapid valve movements associated with the removal of some of the mantle cavity water (see fig. 8a). During exposure the valves remained apart, with the mantle edges visible. However, C.glaucum from the Crouch or from the lagoon population at Widewater do not show this behaviour in air, but clamp the valves together (fig.8b).

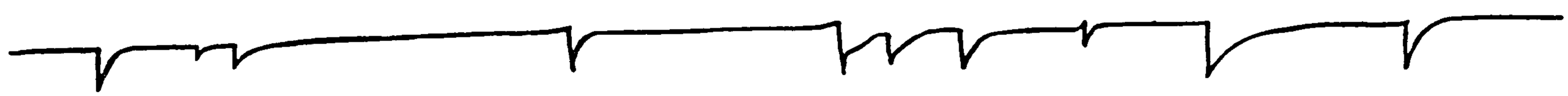
Fig - 7

A) VALVE MOVEMENTS IN WATER.

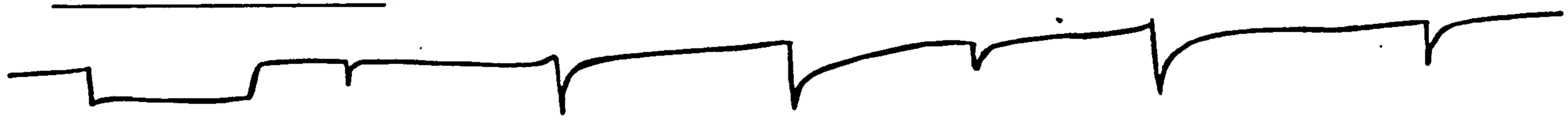
i

C.EDULE. each trace = 50 minutes.

ii



C. GLAUCUM.



KYMOGRAPH TRACES OF THE BEHAVIOR OF THE COCKLES C.EDULE AND C.GLAUCUM.

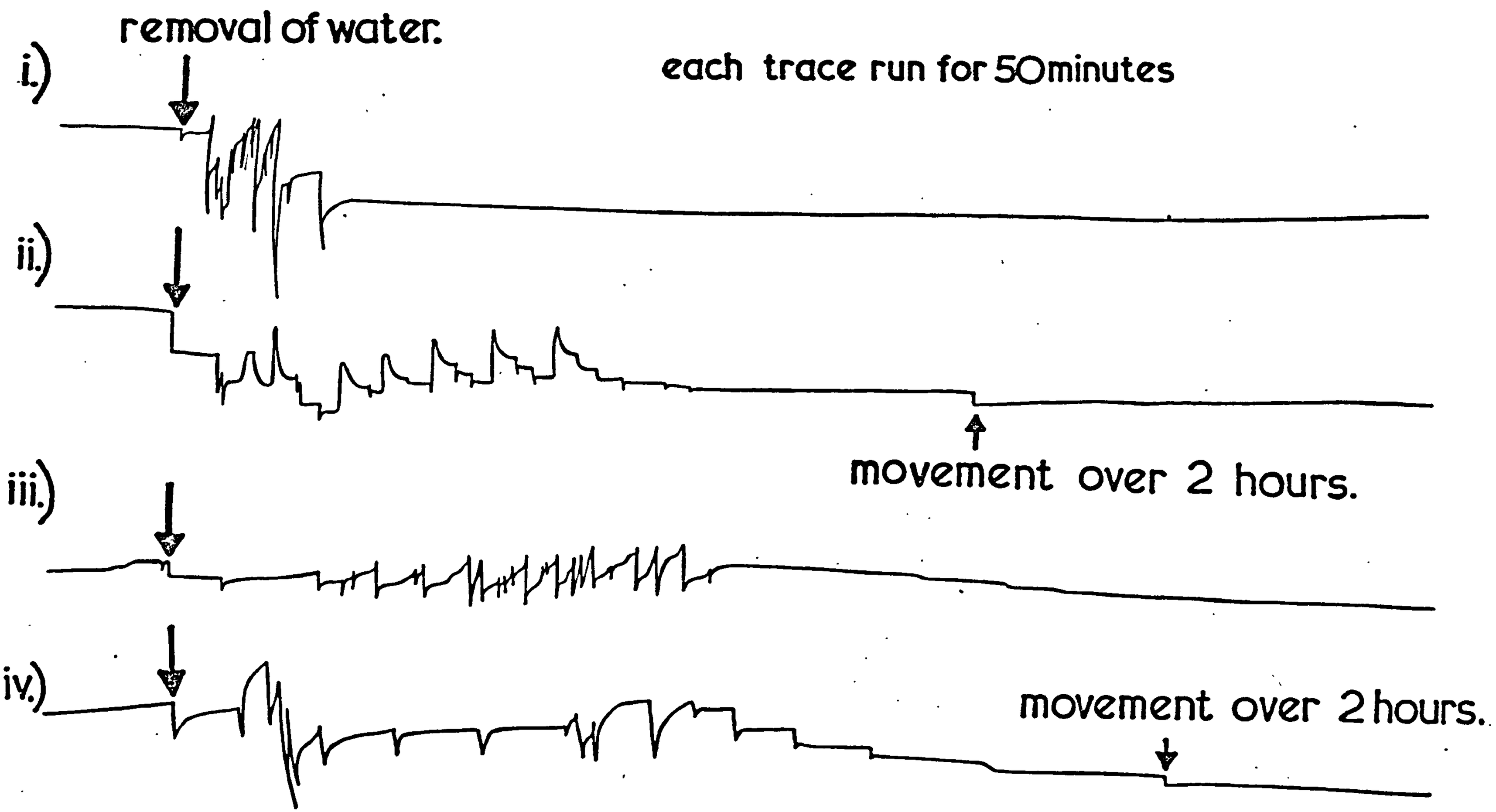
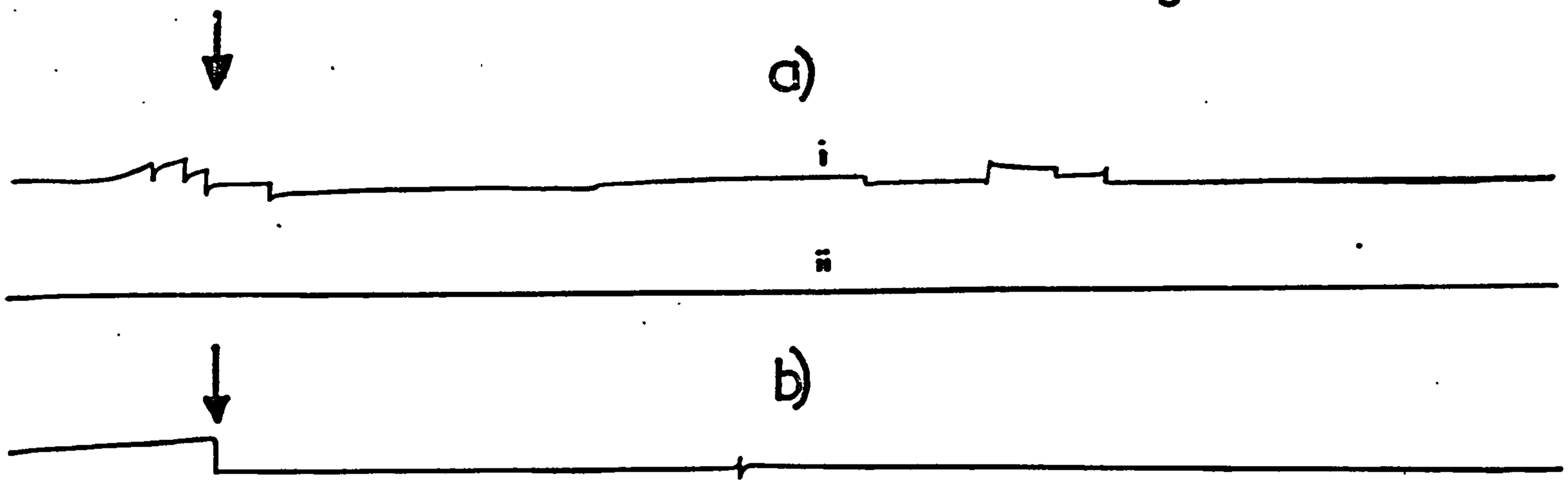
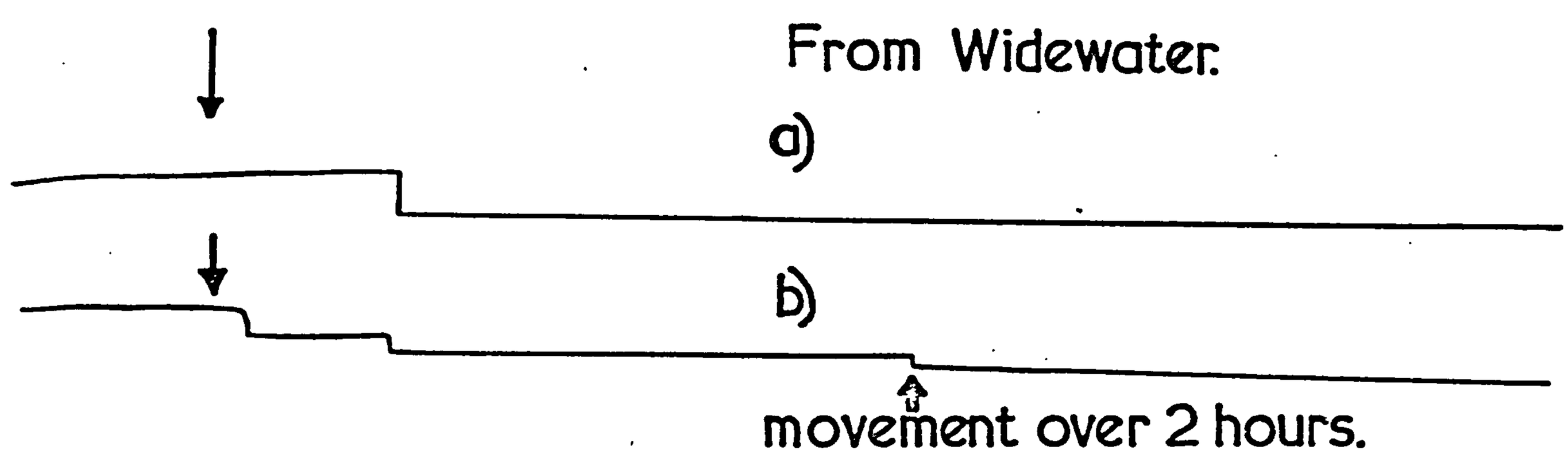


Fig - 8a)

BEHAVIOUR OF C.EDULE ON REMOVAL OF WATER.





each trace = 50 minutes

Fig - 8b)

BEHAVIOUR OF C.GLAUCUM ON REMOVAL OF WATER.

Table 2

The occurrence of gaping in cockles collected from the Crouch mixed population.

(A) C.EDULE - number examined = 31

	Time - hours.					
	5 mins.	25 mins.	35 mins.	1 hr.	1½ hrs.	2¾ hrs.
Numbers gaping:-	19	20	18	18	22	23
Numbers partially gaping:-	6	5	6	7	5	5
Numbers closed:-	6	6	7	6	4	3

(B) C.GLAUCUM - number examined = 32

	Time - hours.					
	5 mins.	25 mins.	35 mins.	1 hr.	1½ hrs.	2¾ hrs.
Numbers gaping:-	2	2	2	2	3*	3*
Numbers partially gaping:-	1	-	-	-	-	2
Numbers closed:-	29	30	30	30	29	27

(* - 2 of 3 gaping individuals were found to be dead at the end of the observations)

On return to water.

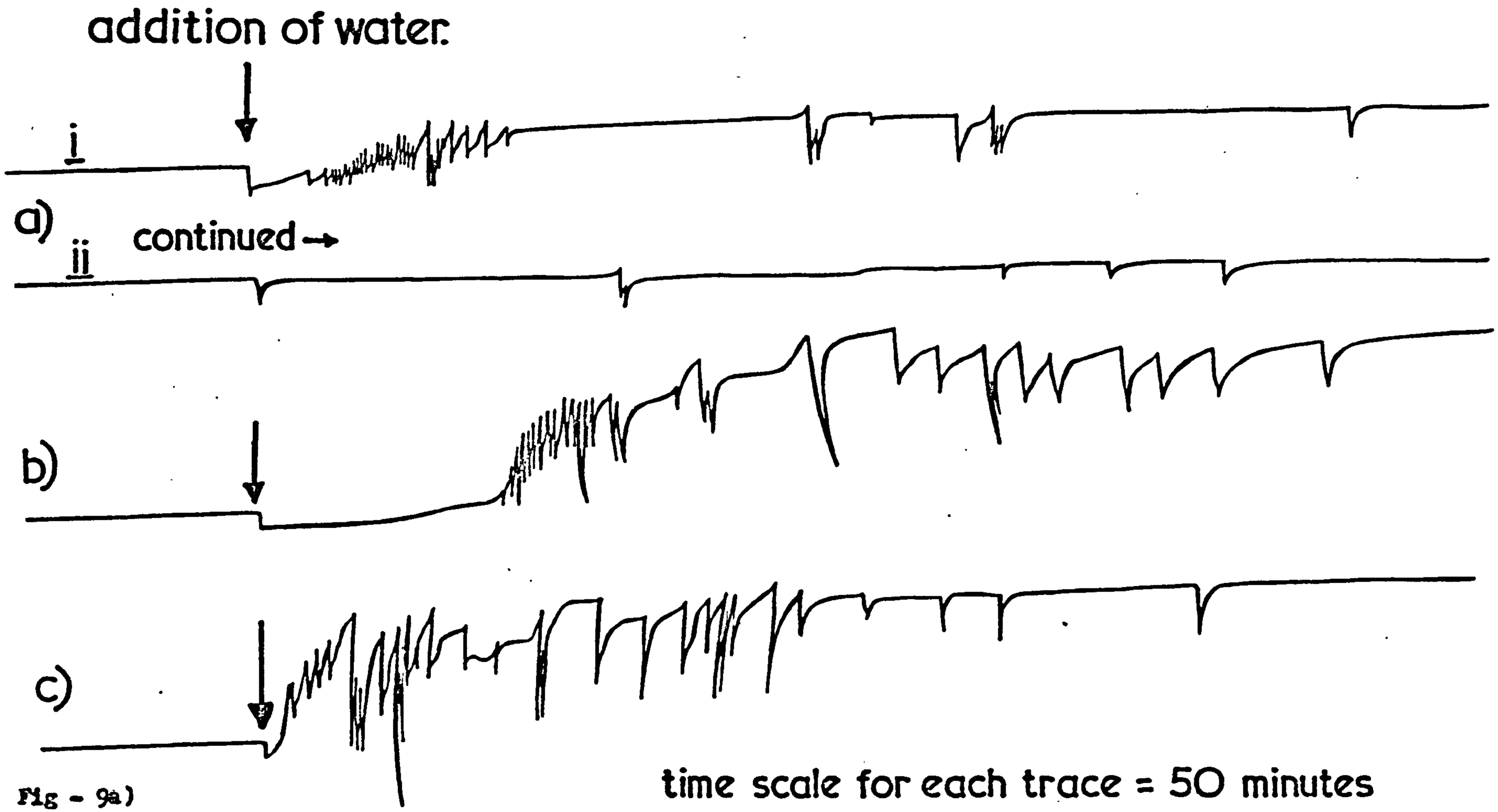
Upon re-immersion C. edule exhibited rapid valve movements which result in the expulsion of gas bubbles from the mantle cavity (fig. 9a). The siphons are then protruded and normal equatic valve movements occur. C. glaucum did not show this behaviour upon re-immersion, the valves slowly parted and the siphons extended, see fig. 9b.

Therefore, upon exposure during low tide, C. edule actively takes an air bubble into the mantle cavity, and upon re-immersion removes this bubble. Such 'controlled behaviour' is consistent with aerial respiration and parallels the adaptations displayed by shore barnacles (Barnes & Barnes, 1957; Barnes & Reese,, 1960). The trochid Monodonta lineata is also recorded to release a string of small gass bubbles upon re-immersion after exposure (Micallef, 1966) and this behaviour is less regularly displayed by many other intertidal gastropods. The 'erratic' behaviour exhibited by the sub-littoral barnacle Balanus crenatus upon exposure to air (Barnes & Barnes, 1957) is similar to the behaviour of C. glaucum upon extreme exposure.

Respiratory significance of mantle cavity air.

Cockles were exposed for two hours, and the volume of air within the mantle cavity was determined by capture and measurement of the bubbles released upon re-immersion. It can be clearly seen in Fig. 10 that C. edule regularly takes air into the mantle cavity during exposure, whereas C. glaucum generally does not, any air taken into the mantle cavity is very small in volume.

To discover whether the gas bubbles within the mantle cavity have a respiratory significance, the oxygen content of the bubbles was determined. Cockles were placed in damp substrate and exposed to



time scale for each trace = 50 minutes

Fig - 9a)

BEHAVIOUR OF C.EDULE ON ADDITION OF WATER AFTER 3 HOURS EXPOSURE TO AIR.

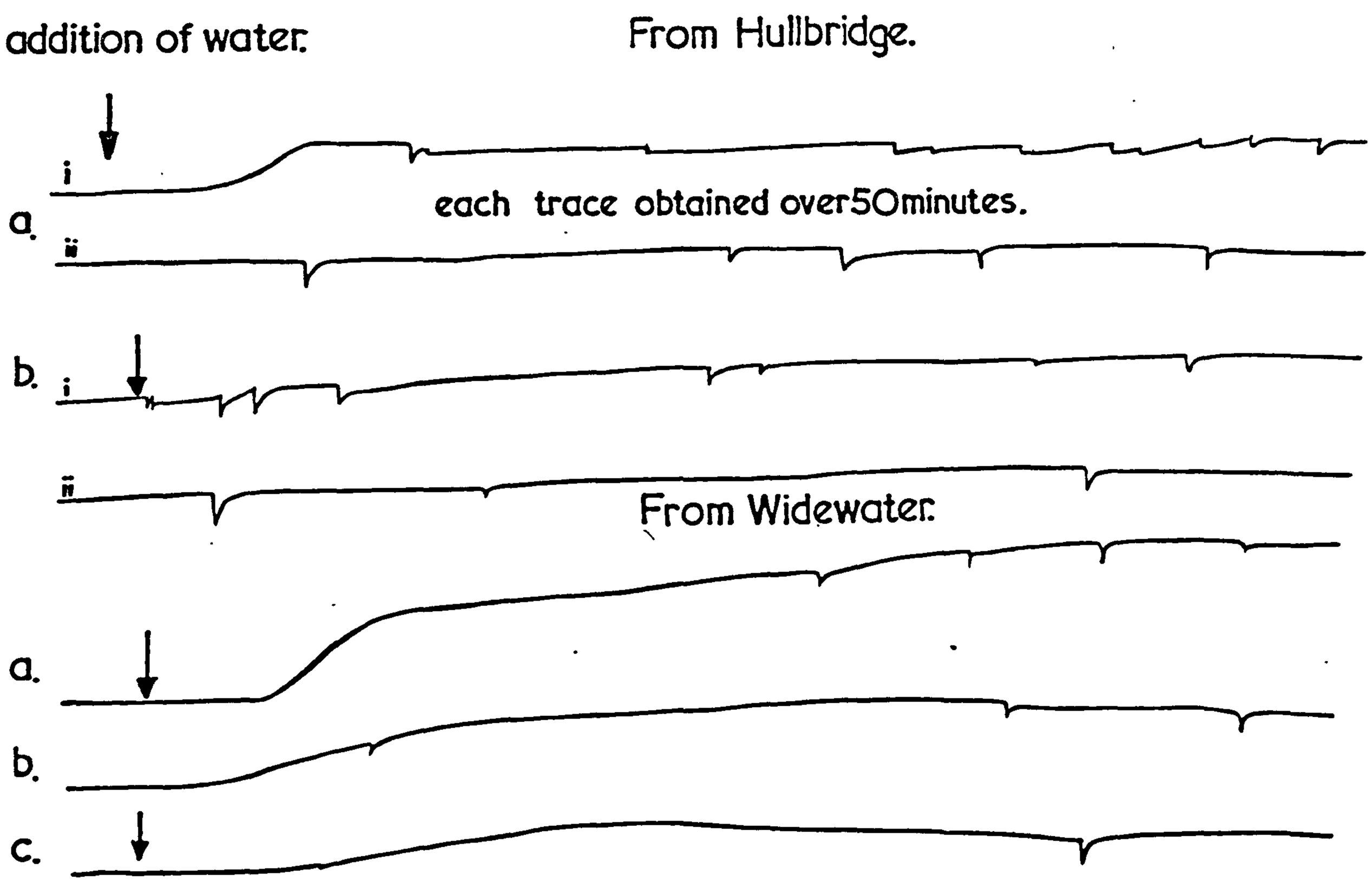


Fig - 9b)

BEHAVIOUR OF C.GLAUCUM ON ADDITION OF WATER AFTER 3 HOURS EXPOSURE TO AIR.

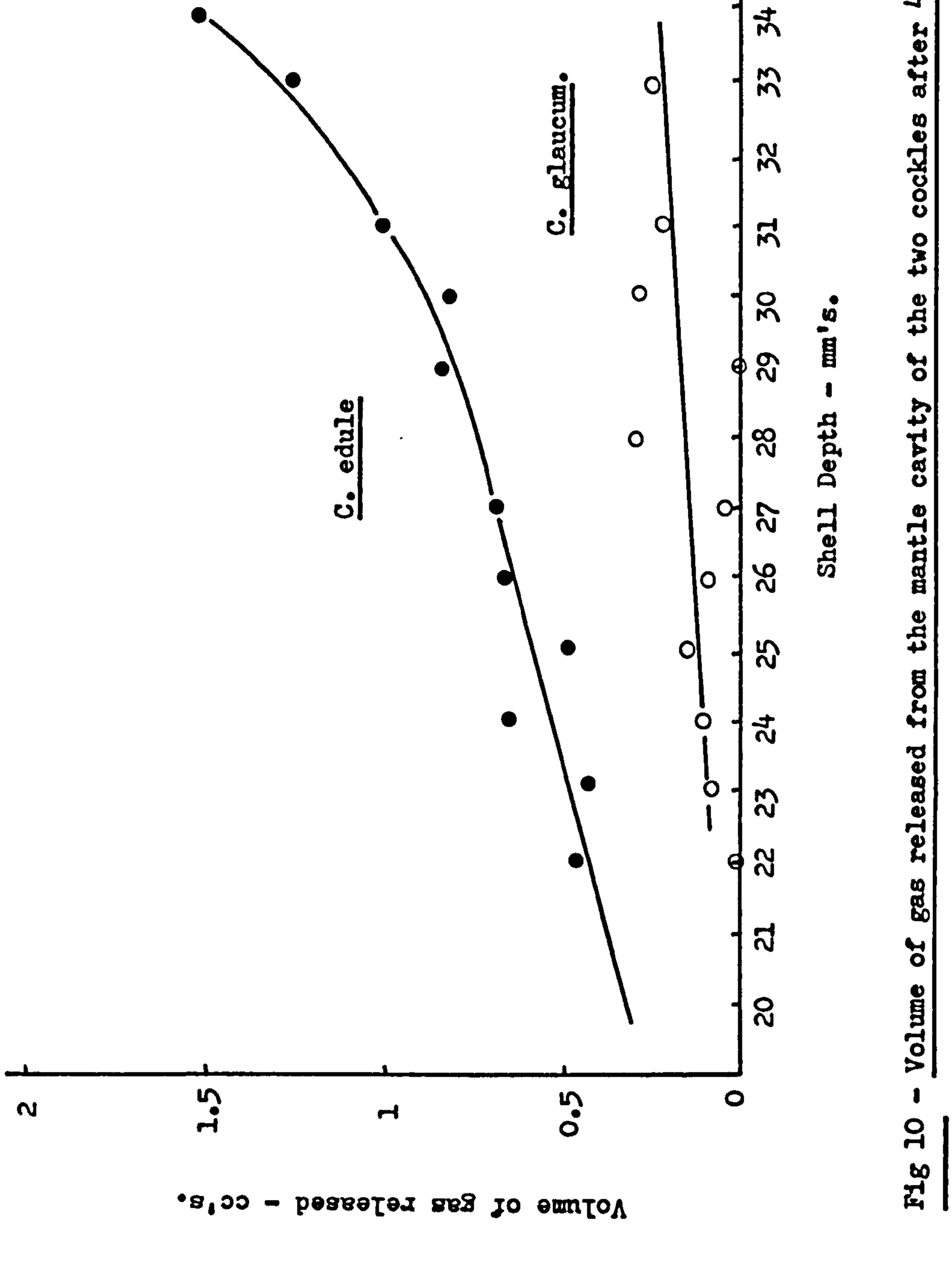


Fig 10 - Volume of gas released from the mantle cavity of the two cockles after 4 hours exposure to aerial conditions.

(means calculated for each mm. size group)

the air at 15°C. At intervals of half an hour, individuals were removed and placed in a beaker of near saturated salt solution. The bubbles released were captured and analysed. (See table 3.)

Reduction of oxygen content of the mantle cavity gas bubbles does occur. However, in C. edule after about 2 hours exposure the oxygen content increased to normal laboratory values. This is correlated with the fact that during exposure interchange between the mantle cavity and the external air becomes possible through the contracted siphons and between the mantle edges. In C. glaucum there were usually no bubbles formed in the mantle cavity, but when they did occur their volume was insignificant compared with the total mantle cavity volume (see Fig. 10).

To prevent equilibration between the mantle cavity air and the environmental air, the shell valves of C. edule were 'clamped' by boss-head clamps after 15 minutes aerial exposure. By examining cockles at intervals and analysing the gas bubbles released, upon removal of the clamps, direct oxygen utilisation could be monitored. The experimental cockles used were of similar size between 28-30 mm. shell depth. Over a period of 5 hours the oxygen content of the mantle cavity bubble was reduced to about 2% (see Fig. 11).

Assuming that the rate of depletion of oxygen from the mantle cavity bubble is similar in a 21.5mm. as it is in a 28mm. shell depth cockle, over the first 2 hours some 65% of the gas bubble oxygen is used by the respiration of the cockle (from Fig. 11). A rate of oxygen uptake per unit time can therefore be calculated:

A 100mg. dry weight cockle ≙ 21.mm. shell depth.

Table 3 - Oxygen content of gas bubbles released from cockles after various periods of exposure.

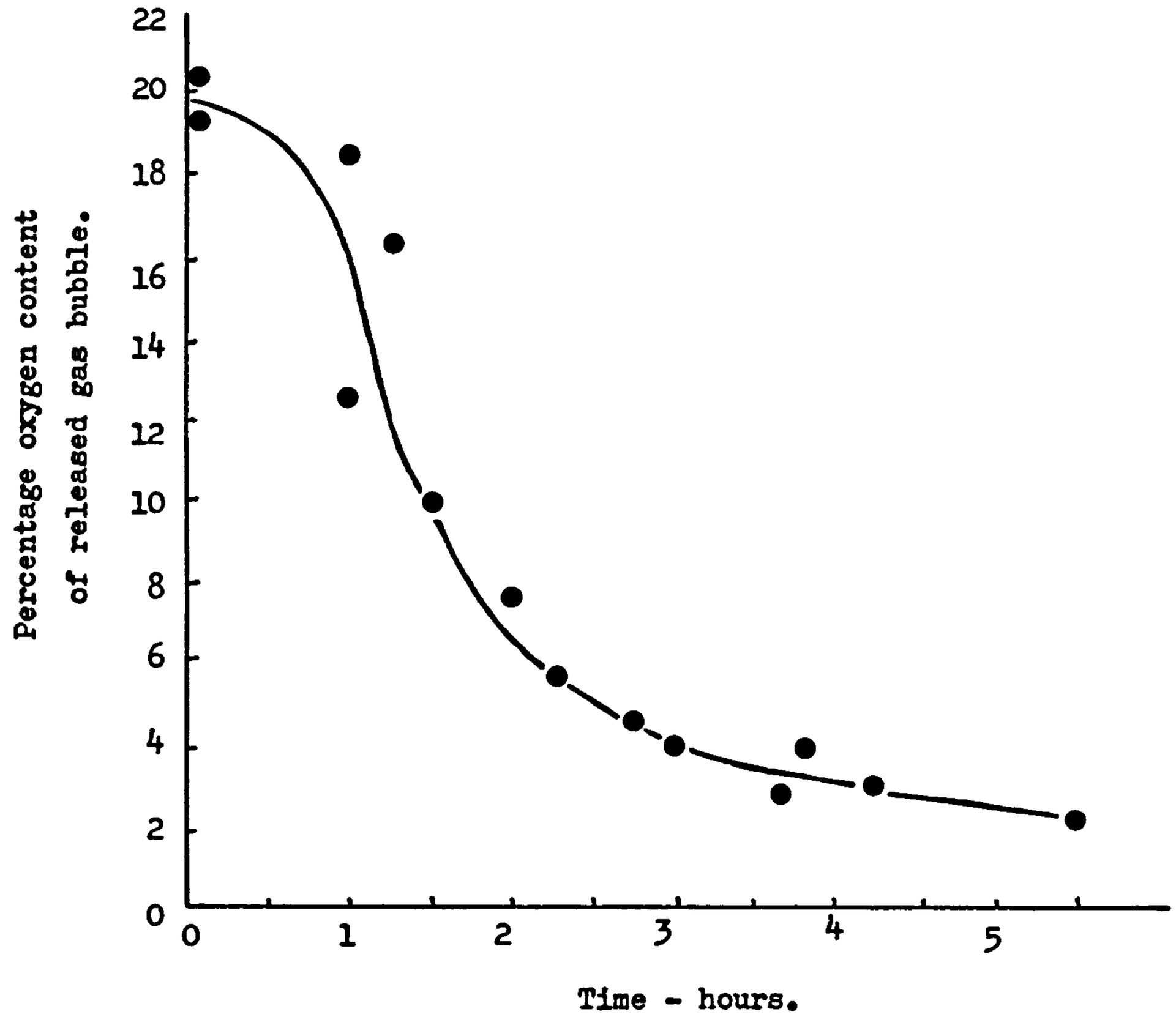
A) Cerastoderma edule

Length of aerial exposure	Percentage oxygen content	Laboratory air controls
½ hr.	20.20	20.89 %
1 hr.	18.66	
1½ hrs.	17.77	
2 hrs.	13.60 (small bubble)	20.72 %
2½ hrs.	9.59 (" ")	
3 hrs.	19.38	21.21 %
4 hrs.	17.75	
5 hrs	20.75	20.56 %

B) Cerastoderma glaucum

Length of aerial exposure	Percentage oxygen content	Laboratory air controls
½ hr.	- (no bubble released)	21.30 %
1 hr.	- (" " ")	
2 hrs.	9.45 (v. small bubble-78µl)	
2½ hrs.	- (no bubble released)	20.82 %
3 hrs.	- (" " ")	
3½ hrs.	- (" " ")	
4 hrs.	14.24 (v. small bubble-150µl)	
5 hrs.	- (no bubble released)	20.45 %
5½ hrs	- (" " ")	
6 hrs.	20.90 (mantle cavity fluid drained from cockle)	
6½ hrs.	- (no bubble released)	21.23 %

Fig 11 - Decrease of percentage oxygen in the mantle cavity gas bubble of 'clamped' C. edule.



The air bubble contained in mantle cavity of cockle of this depth $\simeq$ 0.4 cc's = 400 μ 1. (from Fig. 10).

As over 2 hours 65% of the total oxygen is consumed by the cockle, and as an air bubble of 400 μ 1 contains 80 μ 1 of O_2:

The oxygen utilised in 2 hours = $\frac{80 \times 65}{100}$ μ 1.

Therefore oxygenuptake = $\frac{80 \times 65}{200}$ μ 10_2 /hr./100mg. dry weight.

= $\underline{\underline{0.26}}$ μ 10_2 /mg./hr. for 100mg. cockle.

The calculated value of oxygen uptake 0.26 u 10_2 /mg./hr. would be expected to be less than that rate attained in the natural environment, because of reduction of the mantle surface area available for diffusion. Nevertheless, this value is very close to the 'minimal' aquatic rate of 0.30 μ 10_2 /mg./hr. obtained by Newell & Northcroft (1967) for a 100mg. dry weight cockle at 15°C.

The presence of a mantle cavity air bubble in the cockle C. edule is in direct contract to the only other recorded air breathing lamellibranch, the American Modiolus demissus, (Kuenzler, 1961.) In this mussel, water is retained during exposure within the mantle cavity and is not actively removed as it is in C. edule (Lent, 1968). The respiratory value of air in contrast to water in the mantle cavity during exposure is shown below:

For a 100mg. C. edule the mantle cavity fluid volume $\simeq$ 1,000 μ 1

The size of the air bubble = 400 μ 1

600 μ 1 of sea water is still retained within the mantle cavity.

The quantity of oxygen in sea water of 34.33‰ salinity at 15°C. = 6.00 μ 10_2 /m1 (Krogh, 1941).

Assuming a metabolic oxygen consumption for a 100 mg. cockle of 26 μ 10_2 / hr.

If the mantle cavity only contains water and there is not renewal there would be sufficient oxygen for:

$$6.0 \ \frac{x\ 60}{26} \text{ minutes of aerobic metabolism.}$$

$$= \underline{13.8 \text{ minutes.}}$$

But if the mantle cavity contains air the total oxygen available would be:

From air		From water
$\frac{80}{26}$ hrs.	+	$(6.0 \times 0.6) \times \frac{60}{26}$ minutes
= 3 hrs. 5 minutes	+	8.3 minutes

∴Total = 3 hrs. 13.3 minutes of aerobic respiration.

Thus C. edule by its behavioural adaptations has at least 3 hours 13 minutes oxygen supply at 15°C., whereas C. glaucum, assuming an oxygen consumption of a similar rate, has only sufficient oxygen for about 14 minutes aerobic respiration. C. glaucum by remaining closed during exposure must be able to tolerate anerobic conditions within the mantle cavity, whilst C. edule, by renewal of mantle cavity air by diffusion need not suffer any such oxygen lack during periods of normal exposure.

Whole Body Respiration Rates

The rates of oxygen uptake determined in water for C. edule and C. glaucum were found to be very variable, even for individuals of similar sizes. Newell & Northcroft (1967) recogniced that many different respiratory rates are produced by poikilotherms depending upon their activity, and plotted these rates between 'maximum' and 'minimum' regression lines. Newell has further suggested (Newell, 1970) that th

maximal level of respiration defines the 'active' rate whilst the regression line fitted to the minimal points approximates to the 'standard' rate.

In this study a single rate over a period of at least 20 minutes, more usually 30 - 60 minutes, was calculated, and an average rate was determined for each individual in water, in air and upon re-immersion.

The aquatic respiratory rates so obtained for both cockle types generally fall within the range of rates determined by Newell & Northcroft (1967) - see fig. 12. However, the maximal rates recorded by Newell & Northcroft were not achieved in this study.

In air, C. edule respired at a rate almost comparable with that attained in water, whereas C. glaucum used almost negligeable quantities of oxygen. Of 39 oxygen uptake rates calculated for C. glaucum in air:

7 gave rates of 0 $\mu l O_2$/ mg/hr.

31 " " 0 - 0.1 $\mu l O_2$/mg/hr.

1 " " 0.1 - 0.15 $\mu l O_2$/mg/hr.

Rates for C. edule of the same size range varied from 0.09 - 0.68 $\mu l O_2$/mg/hr. The logarithmic plotting of the rates for both cockles is shown in fig. 13.

The very low and variable oxygen uptake rates measured for C. glaucum probably represent some oxygen diffusion from the air into the mantle fringes. A larger oxygen uptake is not permitted because fluid is retained within the mantle cavity. The shell valves are usually closely apposed, and thus the surface available for such diffusion is reduced. As the rate obtained for this cockle are well below that rate regarded by Newell & Northcroft to be the 'minimal' (aerobic) rate, and as total cessation of metabolism in this cockle has not been shown to occur upon aerial exposure, it must be suggested that during exposure

Fig 12 - Rates of oxygen consumption of C.edule and C.glaucum obtained in water at 15 °C.

● = C. edule

○ = C. glaucum

= maximum and minimum oxygen uptake rates for C.edule obtained by Newell and Northcroft(1967).

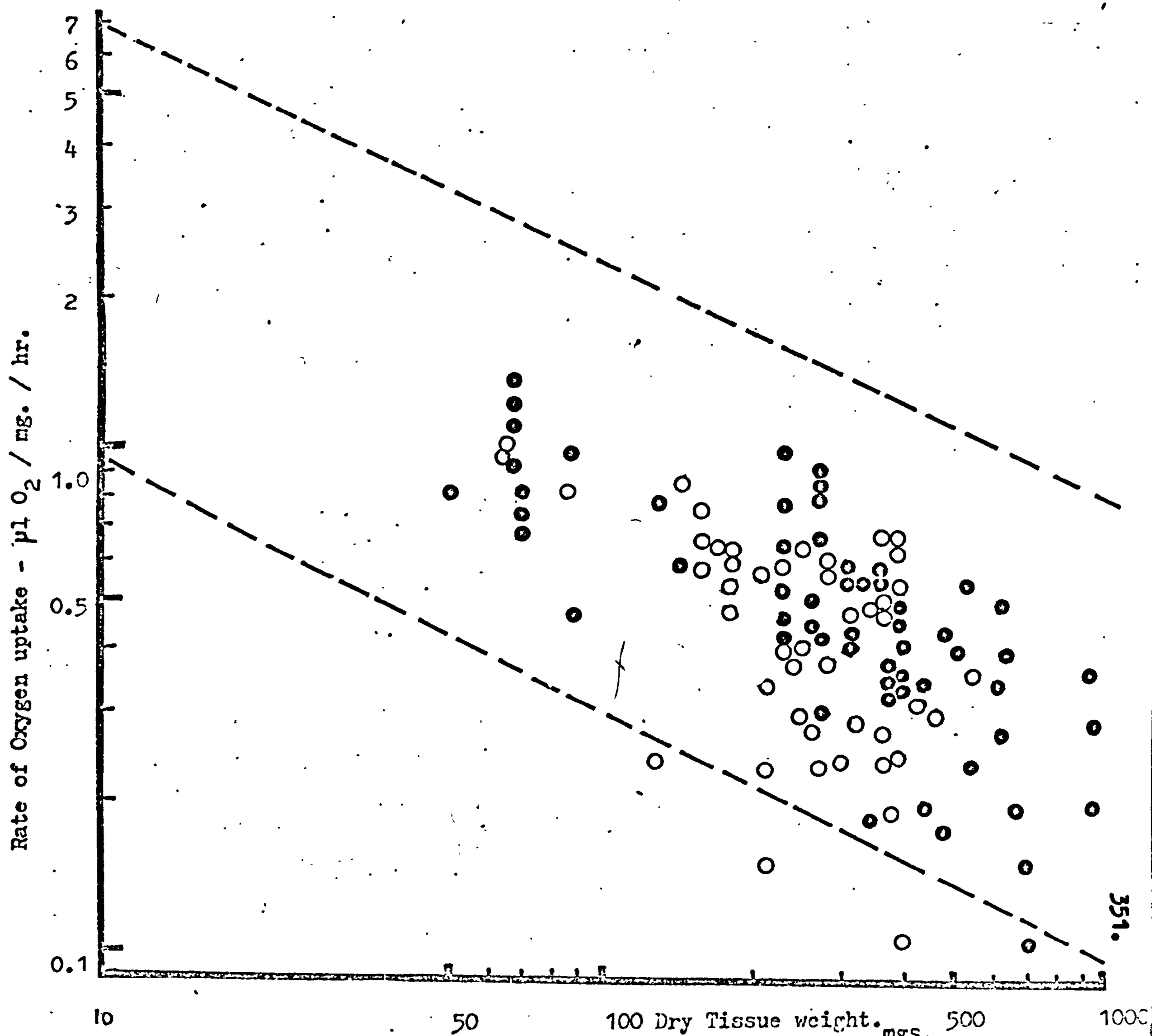
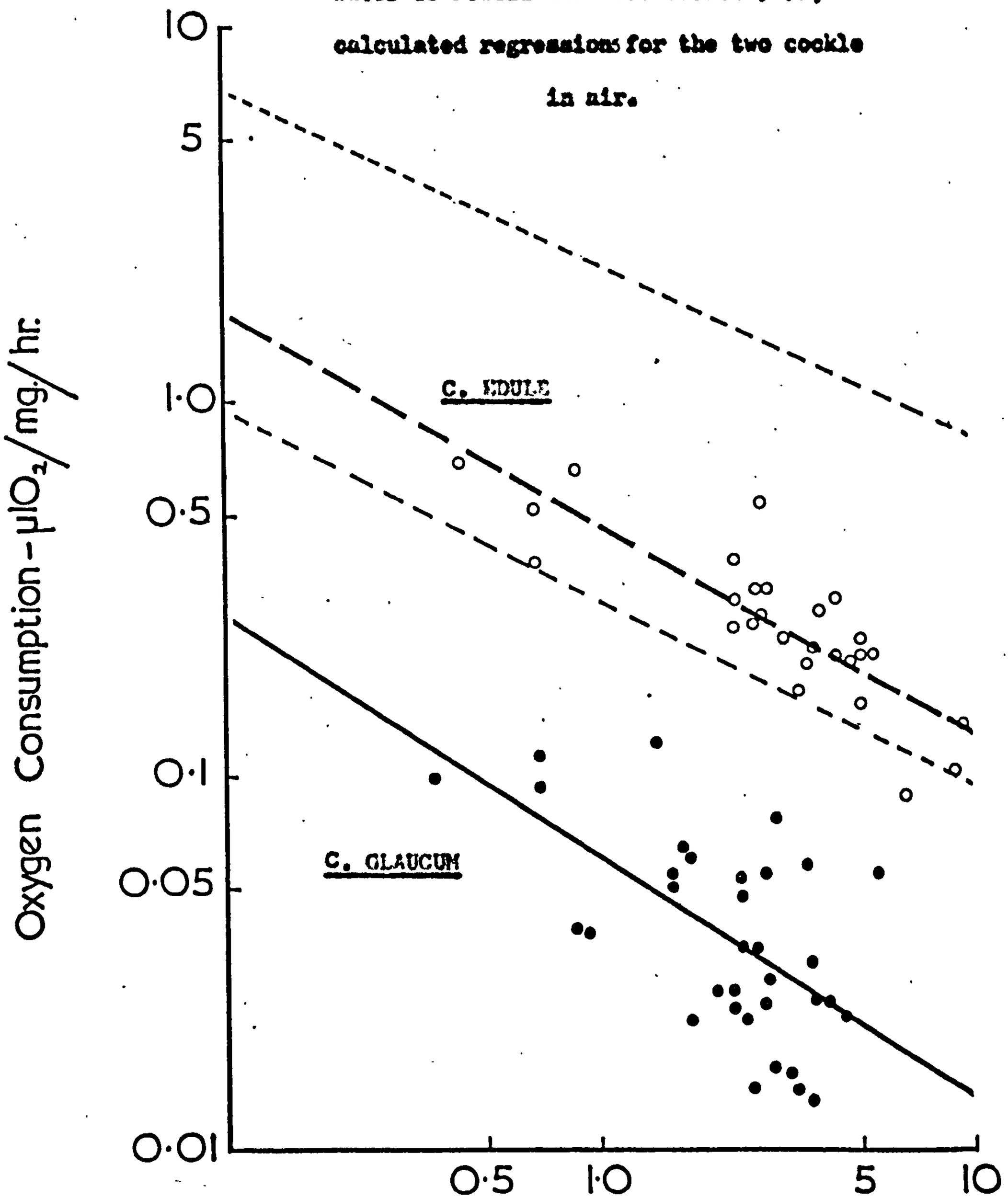


Fig 13 - Respiration rates of C. edule and C. glaucum in air. Included are maximum and minimum rates for C. edule in water of Newell and Northcroft(1967), and calculated regressions for the two cockle in air.



C. glaucum is undergoing anaerobic respiration.

The rate obtained for C. edule in air is probably a low aerobic rate. At the temperature studied, 15°C, the regression coefficient determined in air was no different from the regression coefficients obtained in water (see later). It would thus appear that the diffusion of oxygen through the mantle fringes, mantle and gills, is not limiting. However, as a slight bradycardia has been recognised during exposure, (see earlier, and Trueman, 1967), the rate of oxygen transfer within the body may be insufficient to fully maintain aerobic respiration in all tissues. Nevertheless, as during aerial exposure there are few valve movements (after the initial movements associated with expulsion of water from the mantle cavity), and the ciliary activity of the gills would be expected to be reduced because of the absence of fluid within the mantle cavity, the overall oxygen demands of C. edule must be minimal and may approximate to a 'minimal aerobic' oxygen uptake rate. The measurements above to determine such an inactive respiratory rate have an advantage over the rates obtained for excised cirripedes by Barnes & Barnes (1969), as the experimental animals are larger and give a correspondingly higher rate and remain intact during the experimentation. The oxygen uptake rates obtained on patellid limpets by Davis (1966), although also determined in air, suffer the disadvantage that limpets can, and probably do, exhibit some activity in damp air and thus do not always show a 'minimal' rate.

The calculated regression equations (for method see Davis, 1966, and Appendix VI) and statistical analysis of the oxygen uptake equations are shown on table 4.

The rates of oxygen uptake in water prior to and after 2½ hours aerial exposure in C. edule and C. glaucum are shown in figs. 14 and 15. In both cockles, the rate is greater after exposure. Such an increase in oxygen consumption after aerial exposure has been regarded to be

Table 4.

Regression equations of respiratory rate and dry weight of Cerastoderma edule and Cerastoderma glaucum at 15 °C in air and water.

Cockle type and conditions.	Equation of Regression line. ($Y = a + bX$)	Number of Respiratory rates determined-(N)	Correlation coefficient - (r)	Level of significance
C. glaucum.				
1) In Air. -	$Y = 0.0933 - 0.5915X$	32	0.5878	< 0.001
2) In Water - before aerial exposure -	$Y = 0.8162 - 0.5434X$	29	0.4984	< 0.01
2) In Water - after aerial exposure -	$Y = 1.0367 - 0.5558X$	20	0.9337	< 0.001
C. edule.				
1) In Air -	$Y = 0.8167 - 0.5696X$	27	0.8562	< 0.001
2) In Water - before aerial exposure -	$Y = 0.7487 - 0.4691X$	29	0.6630	< 0.001
3) In Water - after aerial exposure	$Y = 1.1197 - 0.5840X$	26	0.7823	< 0.001

Fig 14 - Rates of aquatic respiration in C.edule before and after $2\frac{1}{2}$ hours of aerial exposure.

□ = after exposure

■ = before exposure

——— = calculated regression line for rate prior to exposure.

▬ ▬ = calculated regression line for rate after exposure.

- - - - - - = maximum and minimum lines of Newell and Northcroft (1967).

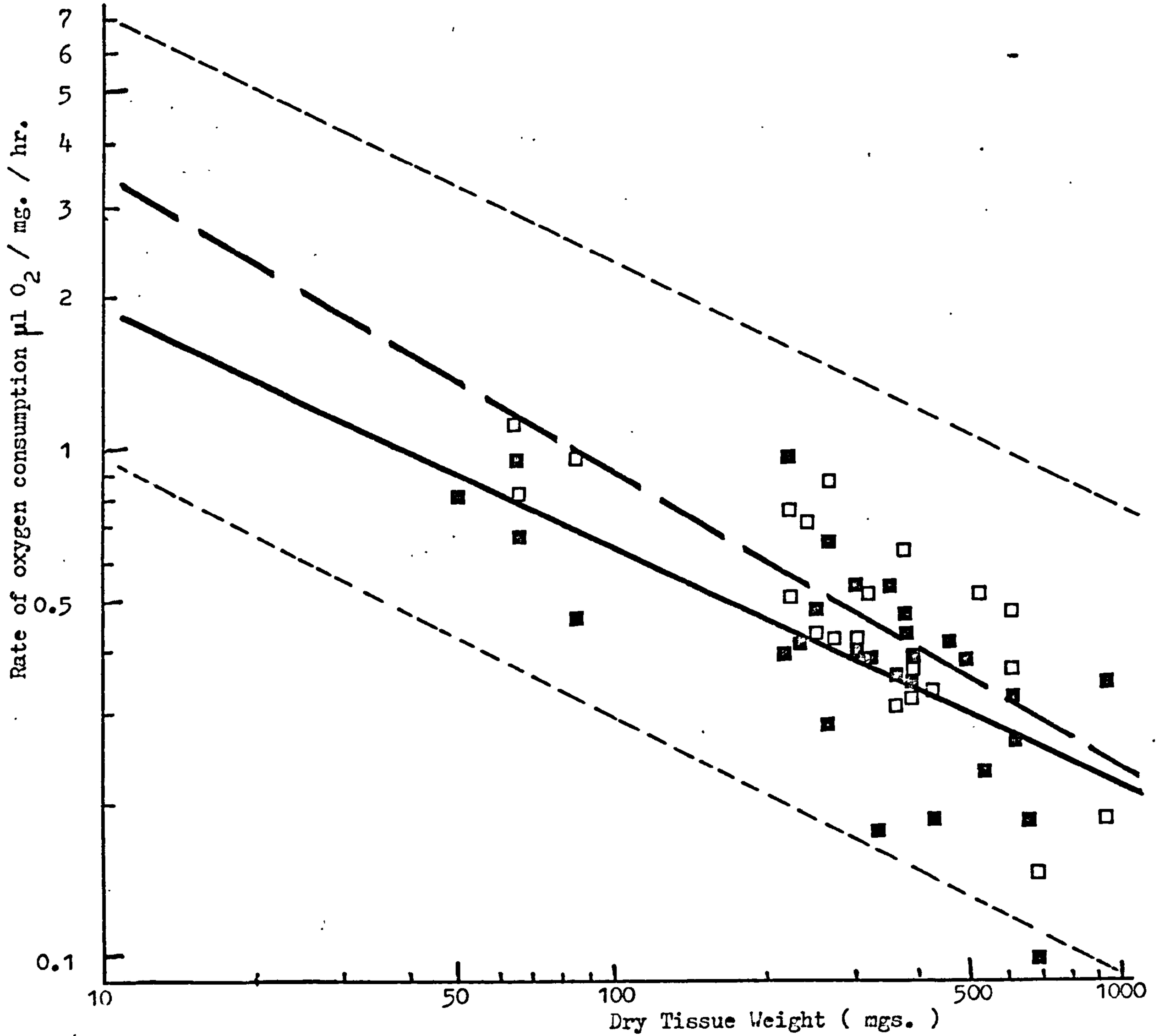


Fig 15 - Rates of aquatic respiration in C.glaucum before and after $2\frac{1}{2}$ hours aerial exposure.

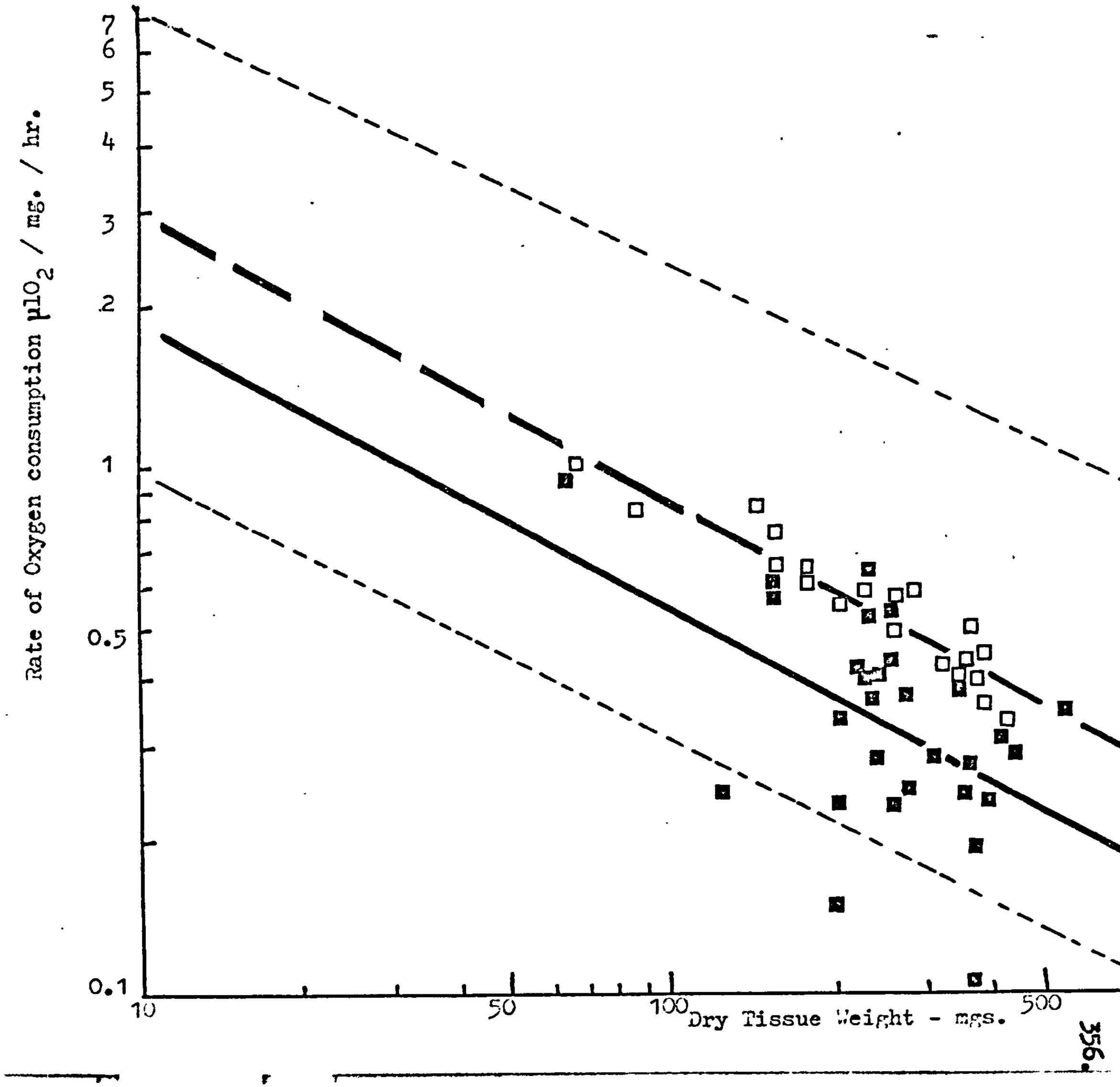
□ = after exposure

■ = before exposure

——— = calculated regression line for rate prior to exposure.

— — — = calculated regression line for rate after exposure.

- - - - - = maximum and minimum lines of Newell and Northcroft (1967)



indicative of repayment of an oxygen debt. However, it has been shown in C. edule that the rate of oxygen uptake during exposure is almost comparable with that obtained in water. Thus, as C. edule air-breaths it is unlikely that an oxygen dept is built up during exposure. C. glaucum, as it does not air breath, probably fits the classical hypothesis of undergoing anaerobic respiration during exposure and repaying an oxygen debt upon reimmersion.

Ignoring the regression equation calculated for the respiration of C. glaucum in air as it is not of interest, the regression coefficients (b' of Davis, 1966) of the remainder of the regression equations, range from -0.5840 to -0.4691 (see table 5 below).

Regression coefficients (b') with 95% confidence limits for the various respiratory rates.

1.	C. glaucum	in air	-0.5915 ± (0.3028)
2.	"	" before exposure	-0.5434 ± (0.3726)
3.	"	" after exposure	-0.5558 ± (0.1027)
4.	C. edule	in air	-0.5696 ± (0.1411)
5.	"	" before exposure	-0.4691 ± (0.2081)
6.	"	" after exposure	-0.5840 ± (0.1946)

Covariance analysis was carried out on each pair of b' values, and no significant differences were found. The sums of the squares and products of the deviations from the regression lines can thus be combined and a common regression coefficient derived (Snedecor, 1961; and as Davis, 1966). The general regression coefficient obtained, (-0.5527 ± 0.1054) can thus be used to describe the relationship between dry weight (mgs.) and respiratory rate ($\mu l O_2$/mg/hr.) for C. edule in air and water, and C. glaucum in water.

Fig 16 - Regression lines for respiratory rates replotted to the common regression coefficent -0.5527 to show differences in elevation.

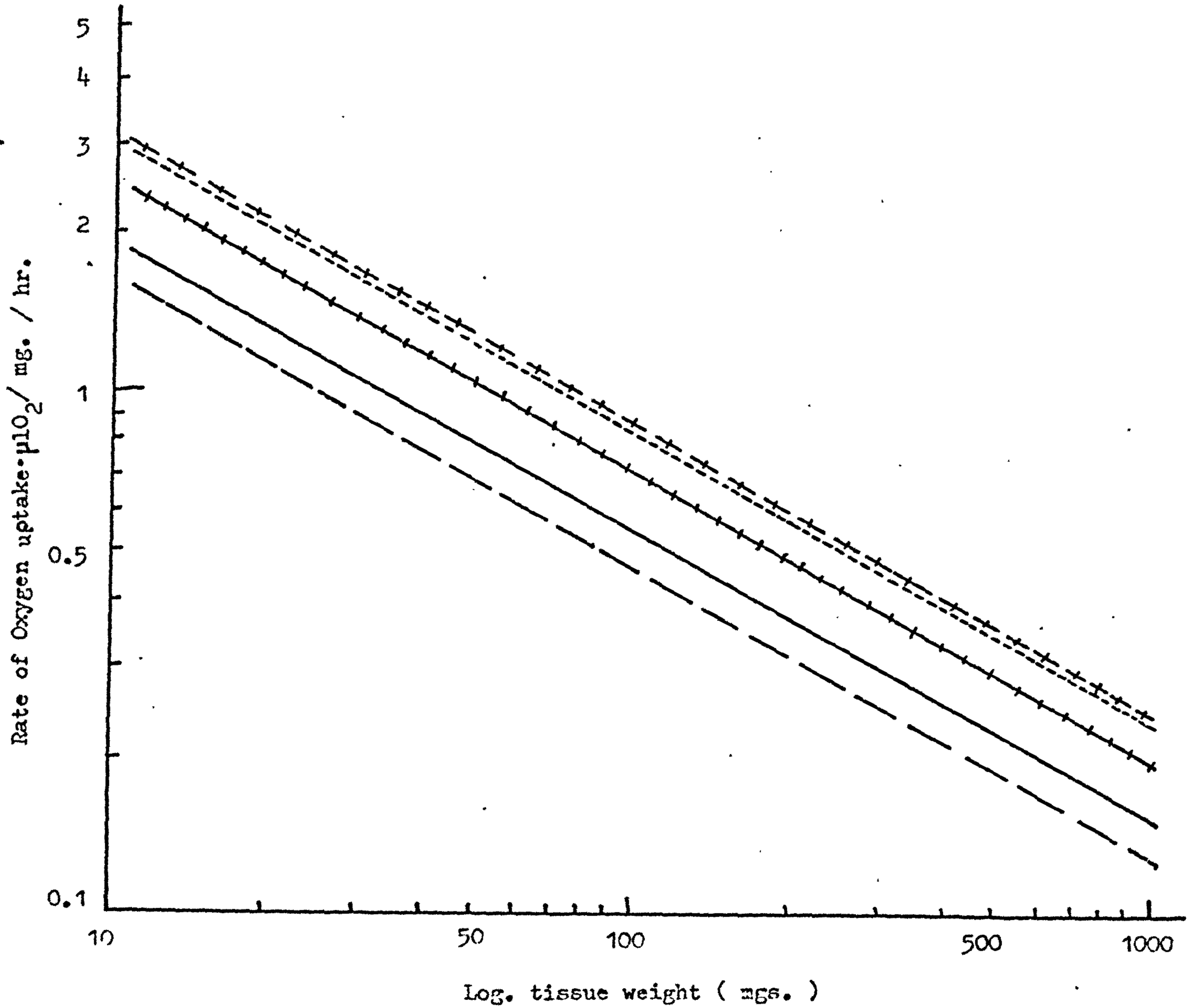
+ + + + = C.glaucum after exposure.

--------- = C.edule " "

+++++++ = C.glaucum before "

——————— = C.edule " "

—— —— = Rate for C.edule in air.



The regression lines were then replotted to this common regression coefficient (as Davis & Walkey, 1966) and are shown on fig. 16. From these graphs it can be seen again that the respiratory rates after exposure are elevated as regards to the rates prior to aerial exposure. Also, the rates obtained after exposure in the two cockles do not differ significantly. It may be suggested that this rate of oxygen uptake nears the maximum rate shown by the two cockles.

Newell (1970, p.358) tabulates the data comparing 'standard' and 'active' rates of oxygen consumption for a variety of intertidal invertebrates. He records, from Newell & Northcroft (1967), that at 15°C a 100 mg. dry weight C. edule gave the following upper and lower rates:

'Standard' rate (= minimal aerobic rate) - 0.3 $\mu l O_2$/mg. dry weight/hr.

'Active' rate (= maximum rate) - 1.9 " " "

An increase of - x 6.3

Regarding the aerial respiratory rate to be indicative of the 'lowest aerobic rate' (or quiescent rate), and the rate in water after exposure to air, to be the 'maximum rate' of oxygen consumption, the following upper and lower rates are obtained for a 100 mg. cockle at 15°C:

Lowest (aerobic) oxygen uptake rate - 0.476 $\mu l O_2$/mg. dry weight/hr.

Highest oxygen uptake rate - 0.895 " " "

An increase of - x 1.9.

This increase approximates to the values obtained for other littoral invertebrates, e.g. Patella vulgata x 1.4 (calculated by Newell from Davis, 1965), and Gammarus oceanicus x 2.5 (calculated by Newell from Halcrow & Boyd, 1967). The maximum respiratory rate obtained in this study for C. edule may be low and could prove to be somewhat higher in conditions where for example foot searching movements are taking place.

Within substrate, in the conditions used in these experiments the cockles remain relatively stationary. Thamdrup (1939) who first realised the importance of aerial respiration in the common cockle calculated that the respiratory rate in air was 51.5% that in water, and thus the work above agrees closely with the early work of Thamdrup.

The comparison of total body respiration in air for C. edule with the rate obtained of oxygen uptake from the mantle cavity gas bubble, provides evidence of the importance of the mantle, probably more especially the mantle fringes, in respiration of lamellibranchs. The rate of oxygen uptake from the mantle cavity gas bubble was calculated as 0.26 $\mu l O_2$/mg/hr. for a 100 mg. dry weight cockle (see earlier). From the whole body respiration figures, this rate is increased to 0.48 $\mu l O_2$/mg/hr. The former value obtained for uptake from the mantle cavity gas bubble, is probably regulated by the surface area of the bubble available for diffusion into the tissues. However, as this rate was calculated over the first two hours of the cockle being 'clamped', the oxygen content is unlikely to be in itself limiting. The difference in rates, 0.22 $\mu l O_2$/mg/hr. (46% of total aerial respiratory rate), reflects the importance of oxygen diffusion through the mantle edges. In water of low oxygen saturation pressures the mantle may be more important than generally realised as a site for oxygen diffusion into the tissues.

Affect of Anaerobic conditions upon the survival of exposed cockles.

Cockles were clamped under water so that they were unable to display their normal behaviour patterns when subsequently exposed to air, and transferred to the damp tanks used previously for the thermal tolerance experiments. The clamped cockles in damp air were unclamped regularly and examined as previously to determine time of death. The mantle cavity water was retained within the cockles during these examinations. The

criterion of death (non-contraction of the adductor muscle) was again used as previously. The $L.D_{50}$ at 15°C. was compared with unclamped control animals (see table 6). The mortality times for C. glaucum were little changed by the clamped conditions, but survival of C. edule differed radically compared with the control animals. Therefore C. edule does derive benefit from taking air into the mantle cavity during exposure. C. glaucum does not seem to be very much more tolerant than C. edule of the anaerobic conditions, which must develop within the mantle cavity of the clamped cockles.

Cockles exposed to an environment of oxygen free nitrogen survived as long as clamped individuals (see also table 6). In this anoxic atmosphere C. edule gaped widely and extended the foot frequently. The survival of C. edule in anaerobic conditions was affected to a greater extent than was the survival of C. glaucum. However, survival in these anoxic conditions does indicate that C. edule, as well as displaying air breathing, can in particularly stressed conditions tolerate anaerobic conditions. This feature has also been recognised in littoral air breathing barnacles (Barnes, Barnes & Platigorsky, 1963) and the American air-gaping mussel Modiolus demissus (Lent, 1969).

Table 6 -

Comparison of mortality (as $L.D._{50}$'s) of 'clamped' cockles, cockles in an anaerobic environment and control cockles in air, at 15°C.

	a) Controls	b) Clamped	Difference between a) and b)	c) Nitrogen environment	Difference between a) and c)
C. edule $L.D._{50}$	129hrs.	69hrs.	60hrs.	75hrs.	54hrs.
C. glaucum $L.D._{50}$	86.7hrs.	74hrs.	12.7hrs.	84hrs.	2.7hrs.
Difference between *C.edule* and *C.glaucum*	42.3hrs.	5hrs.		9hrs.	

Discussion

The use of aerial oxygen by intertidal animals has recently been previewed by Newell (1970), and it has been shown that various decapods, polychaetes and intertidal fish are able to utilise aerial oxygen during low tide conditions. The common shore barnacles Balanus balanoides and Chthamalus stellatus air breath upon aerial exposure through a small micropylar opening between the opercular plates (Barnes, Fullayson & Piatigorsky, 1963; Grainger & Newell, 1965).

Of the temperate shore molluscs, Sandison, 1966, investigated the ability of various littorinids and the dog-whelk Thias lapillus to air breath, and noted that even after 3 hours drying in air Littorina saxatilis still respired at a greater rate in air compared with that in water. This littorinid has also been shown to be more active in air (Berry, 1961), and hence its oxygen demand is correspondingly greater in air. Micallef (1966) studied the littoral adaptation of the four trochids: Monodonta lineata, Gibbula umbilicalis, G. cineraria and Callistoma zizyphinum. Of these only M. lineata and G. umbilicalis respired significantly in air; the former respired faster in air above 15°C, whilst the latter respired at about a comparable rate in air and water. The Mediterranean mid-littoral trochid Monodonta turbinata has also been shown to have a higher oxygen consumption in air than in water at temperatures between 15 - 25°C. (Micallef and Banister, 1967).

The respiratory rates of the limpets Patella vulgata and P. aspera have also been measured in air, Davis (1965, 1966). Of the lamellibranchiata only the high shore ribbed mussel Modiolus demissus of the North American east coast has been shown to leave its valves ajar and to air breath upon aerial exposure at low tide, (Kuenzler, 1961), and to display behavioural and physiological adaptations associated with air breathing (Lent ~~1967~~, 1968, 1969).

It was as early as 1935 that Thamdrup first showed that the cockle C. edule was able to use aerial oxygen during exposure and this has subsequently been noted by Linke (1939) and more recently by Kristensen (1956). These latter authorities refer briefly to the fact that the mantle edges of the cockle remain visible between the shell valves and that the mantle cavity is ventilated by air during exposure. Thus, apart from the early calculation by Thamdrup, the air breathing of the common cockle at low tide has not been commonly recognised.

The British littoral barnacles, Balanus balanoides and Chthamalus stellatus (Barnes & Barnes, 1957) and the American stalked barnacle, Polcipes polymerus (Barnes & Reese, 1960) have been shown to exhibit a behavioural reflex upon aerial exposure resulting in the taking of an air bubble into the mantle cavity. This parallels very closely the observed 'controlled' behaviour of C. edule reported here. Morton (1970) further records that some valve movements occur in C. edule during exposure. These would parallel the cirral and opercular plate movements of littoral barnacles recognised by Barnes and Barnes, 1957. In this study, however, no such movements associated with renewal of the mantle cavity bubble were monitored. Instead it was noted that the valves tended to separate more widely upon continued exposure, so that equilibration between mantle cavity gas bubble and the external air becomes possible between the mantle fringes.

It could be argued that an air breathing ability in the cockle C. edule, which is usually buried in substrate, is somewhat academic. In fact, by observation of cockles in sandy-mud habitats, it can be seen that these buried individuals are often air breathing. On such a shore at low tide, the surface sandy layers ~~can~~ may dry out quite considerably

and a cockle can be located by the presence of two small holes in the sand. Through these holes the siphons extend when the tide is flooding the cockle bed. With exposure at low tide, the siphons are retracted within the shell valves but the two holes made by the siphons remain, allowing the formation of a mantle cavity air bubble. If a buried cockle is removed during the period of exposure and placed in water, within two to three minutes, a gas bubble is extruded from the mantle cavity. The mantle edges are also very prominent between the shell valves of these buried individuals. Thus, although the cockle is buried several inches below the surface, air breathing is often taking place. Occasionally, individuals are found lying upon the sand surface and these cockles obviously have every opportunity to air breathe during low tide conditions.

The concept of increased oxygen consumption in lamellibranchs after aerial exposure associated with repayment of an oxygen debt would seem to require re-examination. Such a 'debt' has previously been demonstrated in Mya arenaria (Van Dam, 1935), Mercenaria (Venus) mercenaria (Dugal, 1939) and Mytilus edulis (Schlieper, 1957). In these lamellibranchs, air breathing would not be expected to occur during low tide conditions. (Thamdrup (1935), however, records an oxygen uptake rate for Mya arenaria in air of 27% that in water). Thus a classic explanation of accumulation of lactic acid during exposure, associated with anaerobis, with a subsequent reconversion of the lactate upon return of oxygenated water, could be upheld. C. glaucum would appear to fall within this category of invertebrate. The air-breathing littoral barnacles do not exhibit an increased oxygen consumption after exposure (Barnes, Finlayson and Piatigorsky, 1963); in fact, after exposure the rate may be less than prior to exposure, associated with dehydration of the tissues

(Cornelius, 1963). It is suggested here that the increase in oxygen consumption in C. edule after exposure may in fact be due to a need to flush excretory products (not lactic acid), accumulated during exposure, from the tissues and mantle cavity.

The bradycardia noted in C. edule during exposure has been suggested by Trueman (1967) to be correlated with oxygen lack. However, during low tide, oxygen is unlikely to be limiting in this animal. It is far more likely that the accumulation of excretory products is in fact inhibiting the heart rate, not a direct oxygen lack.

Conclusion

It has thus been shown that C. edule exhibits an important behavioural adaptation upon aerial exposure, which allows this littoral animal to air breath. C. glaucum does not exhibit a behaviour pattern upon exposure but acts as a 'passive resistor' during aerial exposure. It is considered likely that the absence of a behavioural reaction to facilitate air breathing and probably other adaptations to littoral life, precludes the upshore extension of this cockle where it occurs on the shore.

REFERENCES

BARNES, H. & BARNES, M., 1957. Resistance to desiccation in intertidal barnacles. Science, Vol. 126, p. 358.

BARNES, H. & BARNES, M., 1969. Seasonal changes in the acutely determined oxygen consumption and effect of temperature for three common Cirripedes, Balanus balanoides (L.), B. balanus (L.) and Chthamalus stellatus (Poli). J. exp. mar. Biol. Ecol., Vol. 4, pp. 36-50.

BARNES, H., FINLAYSON, D.M. & PIATIGORSKY, J., 1963. The effect of desiccation and anaerobic conditions on the behaviour, survival and general metabolism of three common cirripedes. J. anim. Ecol., Vol. 32, pp. 233-252.

BARNES, H. & REESE, E.S., 1960. Behaviour of the stalked intertidal barnacle Pollicipes polymerus (J.B. Sowerby) with special reference to its ecology and distribution. J. Anim. Ecol., Vol. 29, 1960, pp. 169-185.

BERRY, A.J., 1961. Some factors affecting the distribution of Littorina saxatilis (Olivi). J. Anim. Ecol., Vol. 30, pp. 27-45.

BOYDEN, C.R., 1969. Ecology of the cockle Cardium glaucum. Bruguiere. Essex Nat. Vol. 32, part 3, pp. 233-226.

BROEKHUYSEN, G.J., 1940. A preliminary investigation of the importance of desiccation, temperature and salinity as factors controlling the vertical distribution of certain intertidal marine gastropods in False Bay, South Africa. Trans. Roy. Soc. S. Africa, Vol. 28, pp. 225-292.

BRYER, D.W., 1962. Swept plate vortex generator for stirring. Br. Chem. Engng., Vol. 7, pp. 332-335.

CORNELIUS, P.F.S., 1968. Activity of intertidal animals in relation to position on the shore. Ph.D. Thesis, Univ. Lond.

COURTNEY, W.A.M. & NEWELL, R.C., 1965. Ciliary activity and oxygen uptake in Branchiostoma lanceolatum (Pallas). J. exp. Biol., Vol. 43, pp. 1-12.

DAVIS, P.S., 1965. Environmental acclimation in the limpet Patella vulgata L. Nature, Lond., Vol. 205, p. 924.

DAVIS, P.S., 1966. Physiological ecology of Patella I. The effect of body size and temperature on metabolic rate. J. Mar. biol. Ass. U.K., Vol. 46, pp. 647-658.

DAVIS, P.S., 1969. Physiological ecology of Patella. III. Desiccation effects. J. mar. biol. Ass. U.K., Vol. 49, pp. 291-304.

DAVIS, P.S. & WALKEY, M., 1966. The effect of body size and temperature upon oxygen consumption of the cestode Schistocephalus solidus (Müller). Comp. Biochem. Physiol. Vol. 18, pp. 415-425.

DUGAL, L.P., 1939. The use of calcareous shell to buffer the product of anaerobic glycolysis in Venus mercenaria. J. cell. comp. Physiol. Vol. 13, pp. 235-251.

FRAENKEL, G., 1960. Lethal high temperatures for three marine invertibrates, Limulus polyphemus, Littorina littorea and Pagurus longicarpus. Oikos, Vol. 11(2), pp. 171-182.

GRAINGER, F. & NEWELL, G.E., 1965. Aerial respiration in Balanus balanoides. J. mar. biol. Ass. U.K., Vol. 45, pp. 469-479.

GUNTER, G., 1957. Temperature in Treatise on Marine Ecology and Paleoecology (Ecology) Ed. J.W. Hedgpeth, Mem. (67). Geol. Soc. Amer., Vol. 1, pp. 159-184.

HALCROW, K & BOYD, C.M., 1967. The oxygen consumption and swimming activity of the amplipod Gammarus oceanicus at different temperatures. Comp. Biochem. Physiol. Vol. 23, pp. 233-242.

HELM, M.M. & TRUEMAN, E.R., 1967. The effect of exposure on the heart rate of the mussel Mytilus edulis L. Comp. Biochem. Physiol., Vol. 21, pp. 171-177.

HØPNER-PETERSEN, G., 1958. Notes on the growth and biology of the different Cardium species in the Danish brackish water areas. Medd. Dan. Fisk- og Havunders, Ny serie, Vol. 2, no. 22, pp. 1-31.

JØRGENSON, C.B., 1966. The Biology of Suspension Feeding. Pergamon Press, Oxford.

KRUGER, P., 1940. On the ecology of Cardium edule L. Arch Neer. de Zool., Vol. 4, pp. 157-200.

KRISTENSEN, I., 1956. Differences in density and growth in a cockle population in the Dutch Wadden Sea. Arch. Neer. de Zool., Vol. 12, pp. 351-453.

KRISTENSEN, I., 1969. Heart rhythm in Patella and Diodora when exposed to air. Pubbl. staz. Zool. Napoli. Vol. 37, pp. 44-50.

KROGH, A., 1941. The comparative physiology of respiratory mechanisms. (William J. Cooper Foundation Lectures, 1939). Univ. of Penn. Press, Philadelphia.

KUENZLER, E.J., 1961. Structure and energy flow of a mussel population in a Georgia salt marsh. Limnol. Oceanogr, Vol. 6, pp. 191-204.

LENT, C.M., 1968. Air gaping by the ribbed mussel Modiolus demissus (Dillwyn): effects and adaptive significance. Biol. Bull. Wood's Hole, Vol. 134, (1), pp. 60-73.

LENT, C.M., 1969. Adaptations of the ribbed mussel Modiolus demissus (Dillwyn), to the intertidal habitat. A.M. Zoologist, Vol. 9, pp. 283-292.

LINKE, O., 1939. Die Biota des Jadebusenwattes. Helg. Wiss. Meeresunters. Vol. 1, pp. 275.

MICALLEF, H., 1966. The ecology and behaviour of selected intertidal gastropods. Ph.D. Thesis, Univ. of London.

MICALLEF, H. & BANNISTER, A.H., 1967. Aerial and aquatic oxygen consumption of Monodonta turbinata (mollusca, Gastropoda). J. Zool. Lond., Vol. 151, pp. 479-482.

MORTON, B.S., 1970. The tidal rhythm and rhythm of feeding and digestion in Cardium edule. J. mar. biol. Ass. U.K., Vol. 50, pp. 499-512.

NEWELL, G.E., 1964. Physiological aspects of the ecology of intertidal molluscs. Eds. K.M. Wilbur and C.M. Yongo, Academic Press, New York and London, pp. 59-81.

NEWELL, R.C., 1970. Biology of Intertidal Animals. Logos Press Ltd., London.

NEWELL, R.C., & NORTHCROFT, H.R., 1967. A re-interpretation of the effect of temperature on the metabolism of certain marine invertebrates. J. Zool. Lond., Vol. 151, pp. 277-298.

ORR, P.R., 1955. Heat death I. Time - temperature relationships in marine animals. Physiol. Zool., Vol. 28, pp. 290-294.

ORTON, J.H., 1926. On the rate of growth of Cardium edule. Part 1. Experimental observations. J. mar. biol. Ass. U.K., Vol. 14, pp. 239-279.

PICKENS, P.E., 1965. Heart rates of mussels as a function of latitude, intertidal height and acclimation temperature. Physiol. Zool., Vol. 38, pp. 390-405.

RUSSELL, P.J.C., 1969. Studies on the ecology, distribution and morphology of the cockles Cardium edule L. and C. glaucum (Bruguière). Ph.D. Thesis, London.

SANDISON, E.E., 1966. The oxygen consumption of some intertidal gastropods in relation to zonation. J. Zool. Lond., Vol. 149, pp. 163-173.

SCHLIEPER, C., 1957. Comparative study of Asterias rubens and Mytilus edulis from the North Sea (30‰) and the Western Baltic Sea (15‰) Anée. biol. (fase 3-4), Vol. 33, pp. 117-127.

SEGAL, E., 1956. Microgeographic Variation as thermal acclimation in an intertidal mollusc. Bull. Biol. Wood's Hole, Vol. 111, pp. 129-152.

SNEDECOR, G.W. 1961. Statistical Methods applied to Experiments in Agriculture and Biology. p. 398. Iowa State Univ. Press, U.S.A.

TEBBLE, N., 1966. British Bivalve Seashells, pp. 95-108. Trustees of the British Museum (Natural History) London.

THAMDRUP, H.M., 1935. Beiträge zur Ökologie der Wattenfauna auf experimenteller Grundlage. Medd. Komm, Dann. Fisk- og Havunders. Serie Fisk., Vol, 10(2), p. 63.

TRUEMAN, E.R., 1967. Activity and heart rate of bivalve molluscs in their natural habitat. Nature, Vol. 214, pp. 832 - 833.

VAN DAM, L., 1935. On the utilisation of oxygen by Mya arenaria. J. Exp. Biol., Vol. 12, pp. 86-94.

SECTION - IX

SECTION IX

COMPARATIVE BIOCHEMICAL STUDIES BETWEEN THE COCKLES CERASTODERMA EDULE (L) AND CERASTODERMA GLAUCUM (POIRET).

1. Spectrophotometric analysis of acetone extracts of the digestive gland of the two Cerastoderma.

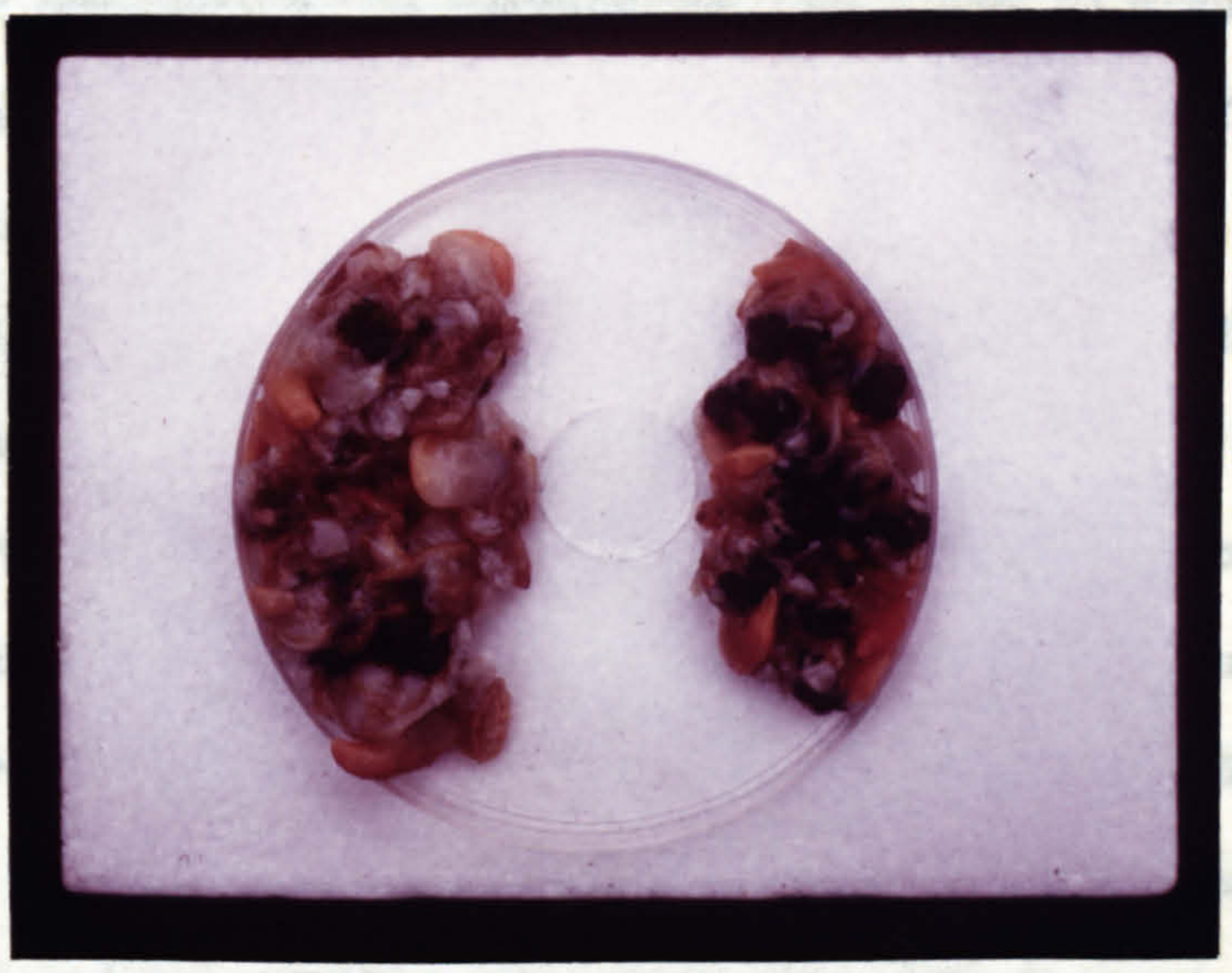
It has been suggested earlier (Boyden, 1969) that the differences in colour of the digestive gland between C. edule and C. glaucum may have taxonomic value in the separation of the two cockles. The significance of this colour variation is discussed in this section.

It has previously been shown in section V 5, that the ratio of dry weight of digestive gland to total dry tissue weight during the winter months is less in C. edule than in C. glaucum. The gland, irrespective of season, is always coloured black in all C. glaucum examined, whether they originate from lagoonal or from mixed localities.

In contrast, the colour of the digestive gland of C. edule is variable (see Plate 1). During starvation in the laboratory, the gland of C. glaucum maintains its colour and size, whilst in C. edule it becomes reduced in size and pale brown in colour. During the late autumn and winter months, the colour of the gland in C. edule is variable, a feature which may be correlated with the amount of food being assimilated by the cockles. Thus, those individuals with food in the intestine usually have digestive glands coloured dark green or brown, whereas those with no visible food in the gut are more often coloured pale brown or fawn. In the spring and early summer, the gland of C.edule increases somewhat in size and takes on a similar form to that maintained by C. glaucum throughout the year. However, the gland is never black, though it may be dark green.

Plate 1

Plate 1 - Photograph of wet tissues of C. edule and C. glaucum showing the black digestive gland of C. glaucum.



C. EDULE C. GLAUCUM

Material and Methods.

To investigate further these differences in pigmentation of the digestive gland of the two cockles, the following procedure was adopted. Chlorophylls and carotenoids, two of the major classes of pigments amongst the many coloured compounds present, were extracted with acetone. For most of these comparative studies, cockles from the mixed Crouch population were used, although occasionally lagoonal C. glaucum were also studied.

The digestive glands from two or three individuals were washed with distilled water to remove excess sea-water, and the surplus water removed. The tissue was then weighed and as near identical weights as possible of digestive glands were used in comparative experiments between the two cockles. The tissue was homogenised in a handblender (glass tissue grinder produced by Gallenkamp Co. Ltd.) for 10 minutes and the pigments were extracted with 10mls. acetone. When the effect of tissue water is taken into consideration, the concentration of acetone would probably be reduced to about 85%. After homogenisation, the larger tissue fragments were removed by filtration through a '454 - celite' filter. The extracted pigments were placed in a 1 cm. light path cuvette and scanned from 800 - 320 nanometres (nm) using a D.B. Beckman Spectrophotometer. The solvent system was selected from the following:- distilled water; methanol + 5% hydrochloric acid (w/v); benzene; ethyl alcohol and acetone. Acetone gave the best definition of peaks, and extracted the pigments rapidly. Also, it could be easily cleared using 'celite'.

Results and Discussion.

A typical scan relating percentage light transmission to wave-

length is shown in Fig. 1. A well defined peak (or two peaks) occur between 685 and 665 nm., smaller reductions in percentage transmission occur between 640 and 560 nm., and, finally, a complete, or near complete, loss of light transmission occurs below about 440 nm., this extinction being associated with the mass of carotenoidal pigments found in the digestive gland. The pattern below 640 nm. was extremely similar in both cockle types and in a variety of other lamellibranch digestive gland extracts also examined.

The peaks at 685 - 665 nm. were of interest as they were obviously due to only one or two pigments and appeared to differ in the two cockles. A typical scan for C. edule is shown on fig. 2. It is immediately noticeable that the main peak in this region occurs at about 685 nm. compared with the 668 nm. single peak found in C. glaucum. These peaks were thought to be caused by chlorophyll obtained from the food of the cockle. It was possible that these peaks were merely reflecting the difference between a lagoonal and a littoral habit, and hence cockles were studied from the Crouch mixed cockle population. It had previously been observed that the digestive gland of C. edule varied during the year and this has tentatively been suggested to be correlated with food availability. A sample of cockles was collected from Hullbridge, River Crouch on the 22.8.68 and the digestive gland pigments were examined immediately upon return to the laboratory, some 2 hours after collection. The remainder of the sample of both Cerastoderma was maintained for several weeks in a constant temperature room at 15°C in a large volume of filtered, regularly changed sea-water.

The absorption spectra of the digestive gland extract of the two cockles examined immediately after collection are shown on Fig. 3. The double peaked form of the spectra is consistent in all extracts

Fig 1 - Absorption spectrum of acetone extract of the Digestive Gland of C.glaucum collected from the Fleet, Dorset on 9. 8. 68
Spectrophotometric scan relating percentage light transmission to wavelength, completed on 10. 8. 68.

377.

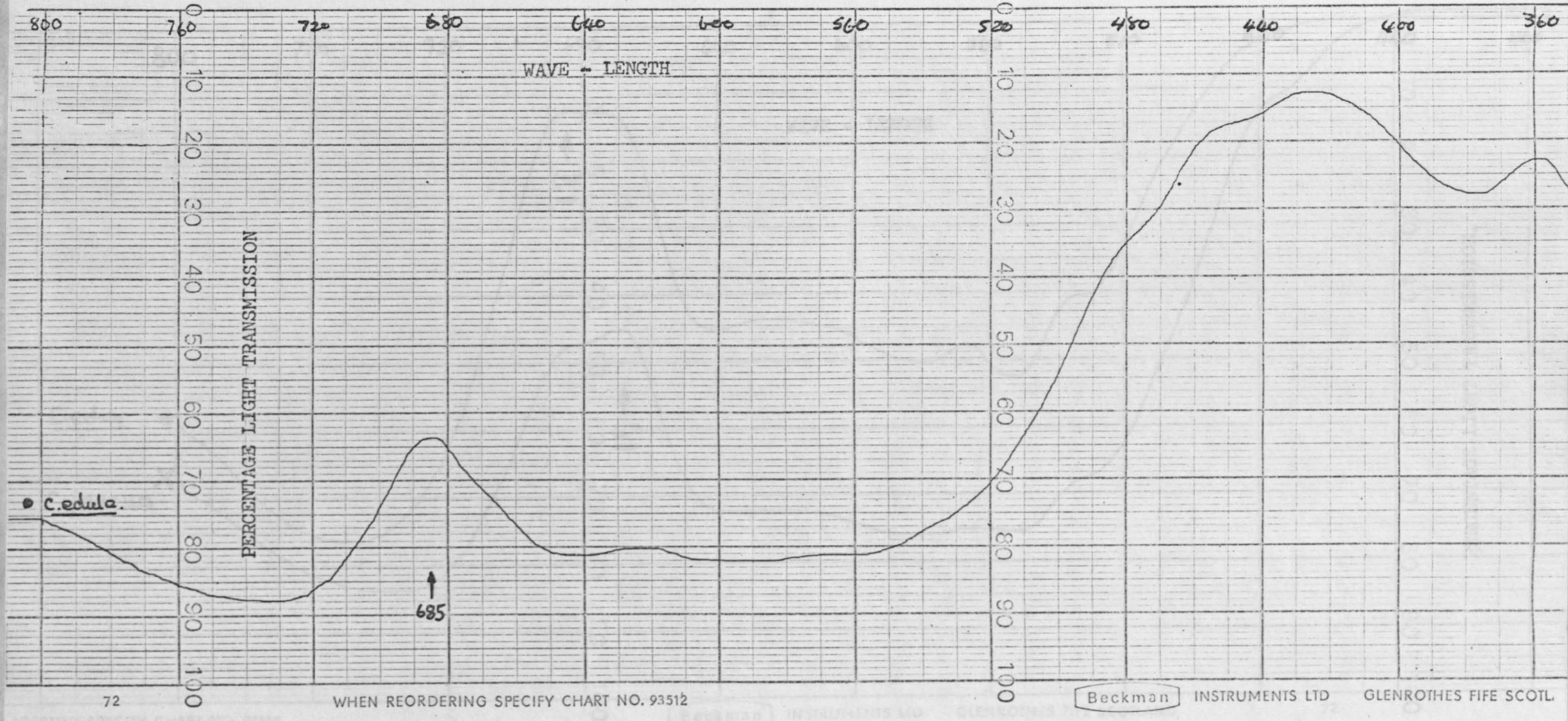


Fig 2 - Absorption spectrum of acetone extract of the digestive gland of C. edule collected from Southend on 14. 8.68. Extract prepared immediately upon return to laboratory.

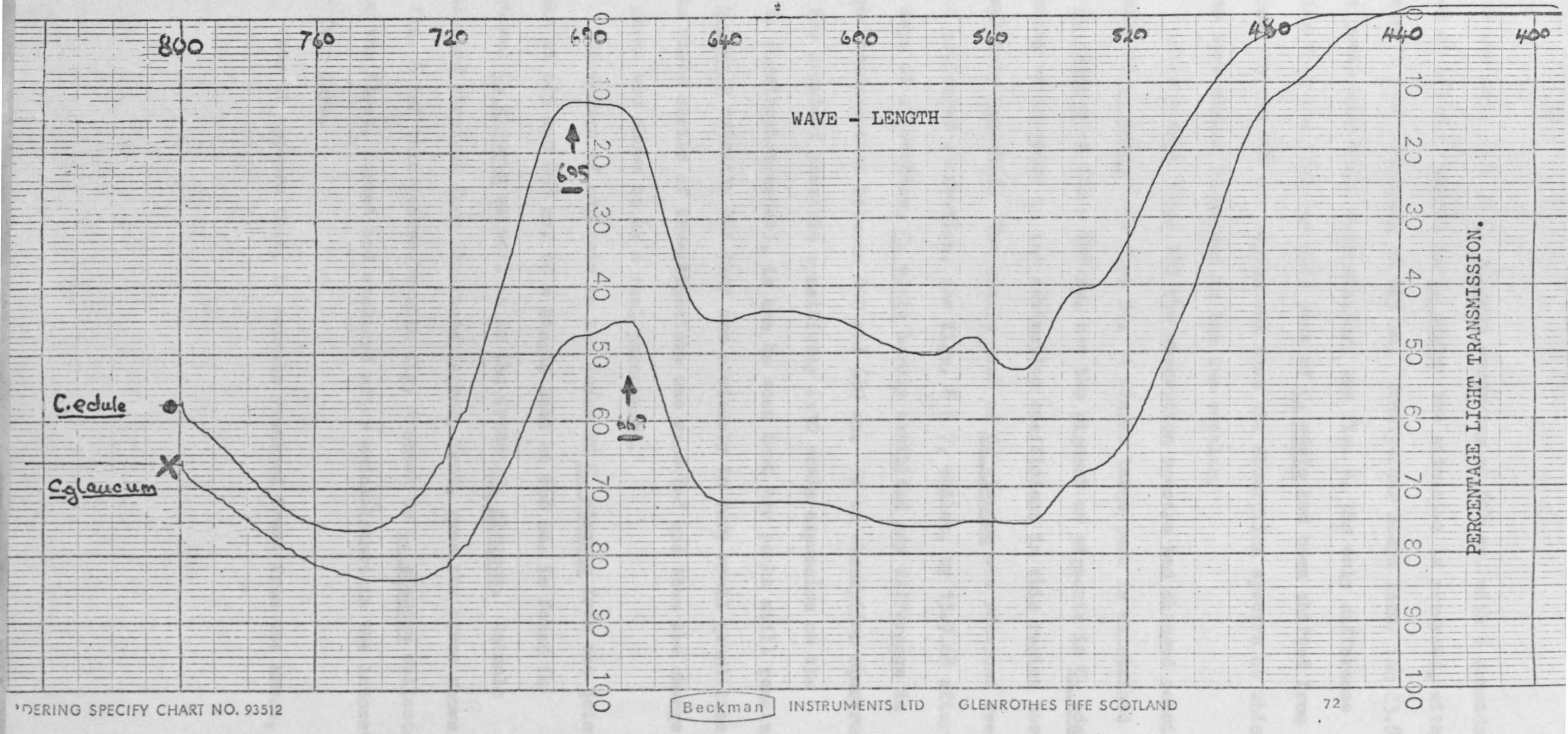


Fig 3 - Comparative absorption spectra of C.edule and C.glaucum collected from the River Crouch estuary on 22. 8.68. Extracts prepared immediately upon return to laboratory.

with the main peak of C. glaucum occurring at 668 nm. with a subsidary peak at 685 nm., whilst in C. edule the situation is reversed, with the main peak occurring at 685 nm. Twenty-four hours later (on 23.8.68), the peaks were still very similar, see fig. 4, the only difference being that the previous main peak of C. edule had been shifted from 685nm. to the 668 nm. region and thus the absorption spectra at this time were almost identical in the two cockles.

After 3 days (25.8.68) the absorption spectra had changed considerably in C. edule (see fig. 5). A single large peak is maintained by C. glaucum at 667 - 668 nm. but the pigment or pigments in C. edule causing an increase in the extinction coefficient in this region have completely vanished. The single peak of C. glaucum was retained even with prolonged starvation, see figs. 6 & 7, whilst, by 13.9.68 after 22 days of starvation, C. edule hardly exhibited any difference in light transmission between 690 and 660 nm. In an absorption spectrum at the greatest possible sensitivity (x10 scale expansion on the U. B. Spectrophotometer), it can be seen that two peaks still remain in C. edule extracts but they are obviously in very small quantities. This whole series of investigations was repeated and thus the change in peaks was shown to be a real phenomenon.

The change of emphasis in the peaks of C. glaucum from the joint peaks at 685 and 668 nm. to a single peak at 668 nm. is found in lagoonal C. glaucum as well as in the Crouch C. glaucum. Animals collected straight from Sheerness lagoon, Kent, gave the curve shown on fig. 8 and this contrasts with fig. 1 which is C. glaucum collected from the Fleet, Dorset and examined after maintenance in the laboratory for four days.

Thus it appears that, in animals examined fresh from the shore,

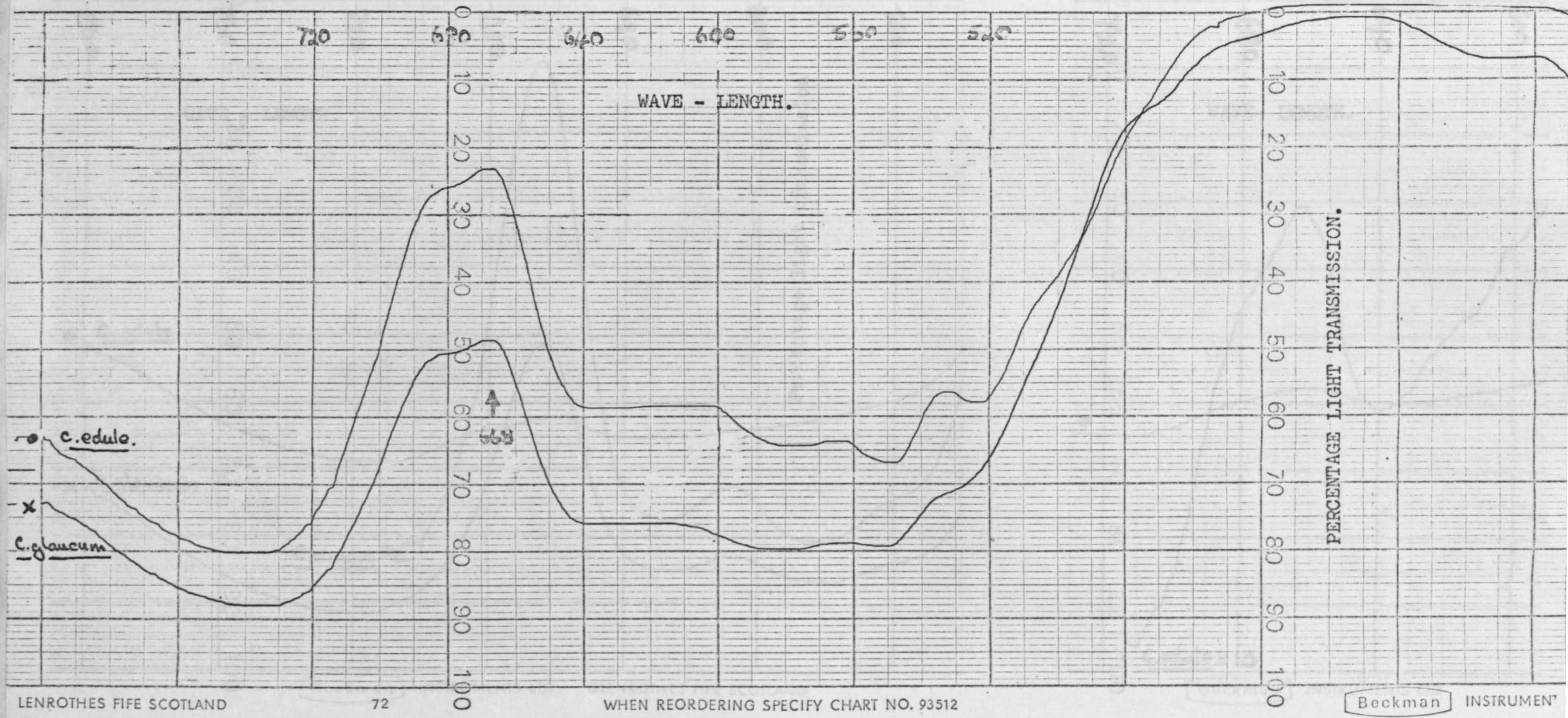
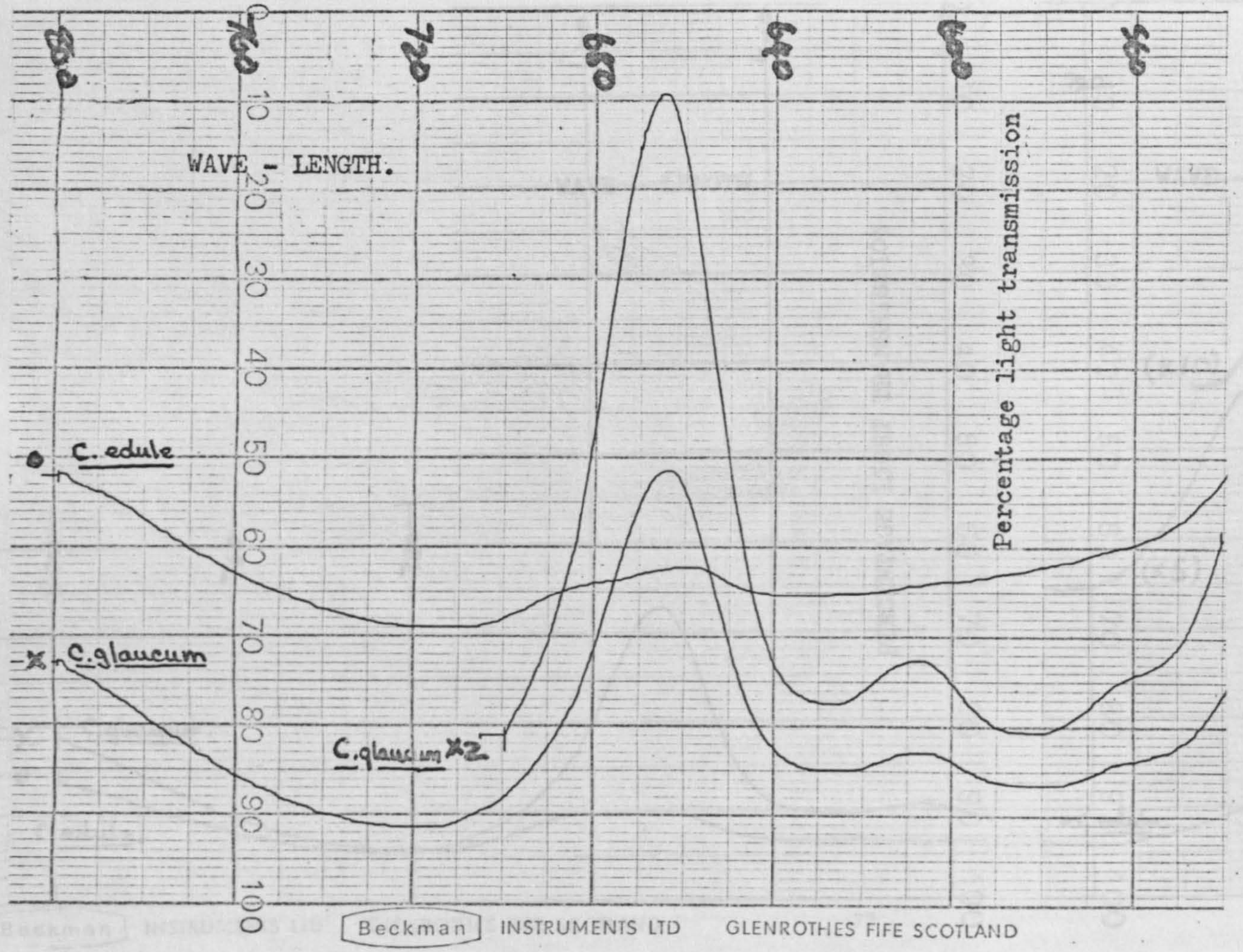


Fig 4 - Absorption spectra of Crouch Cerastoderma collected on 22. 8.68., examined on 23. 8.68 after maintenance in the laboratory for 24 hours.



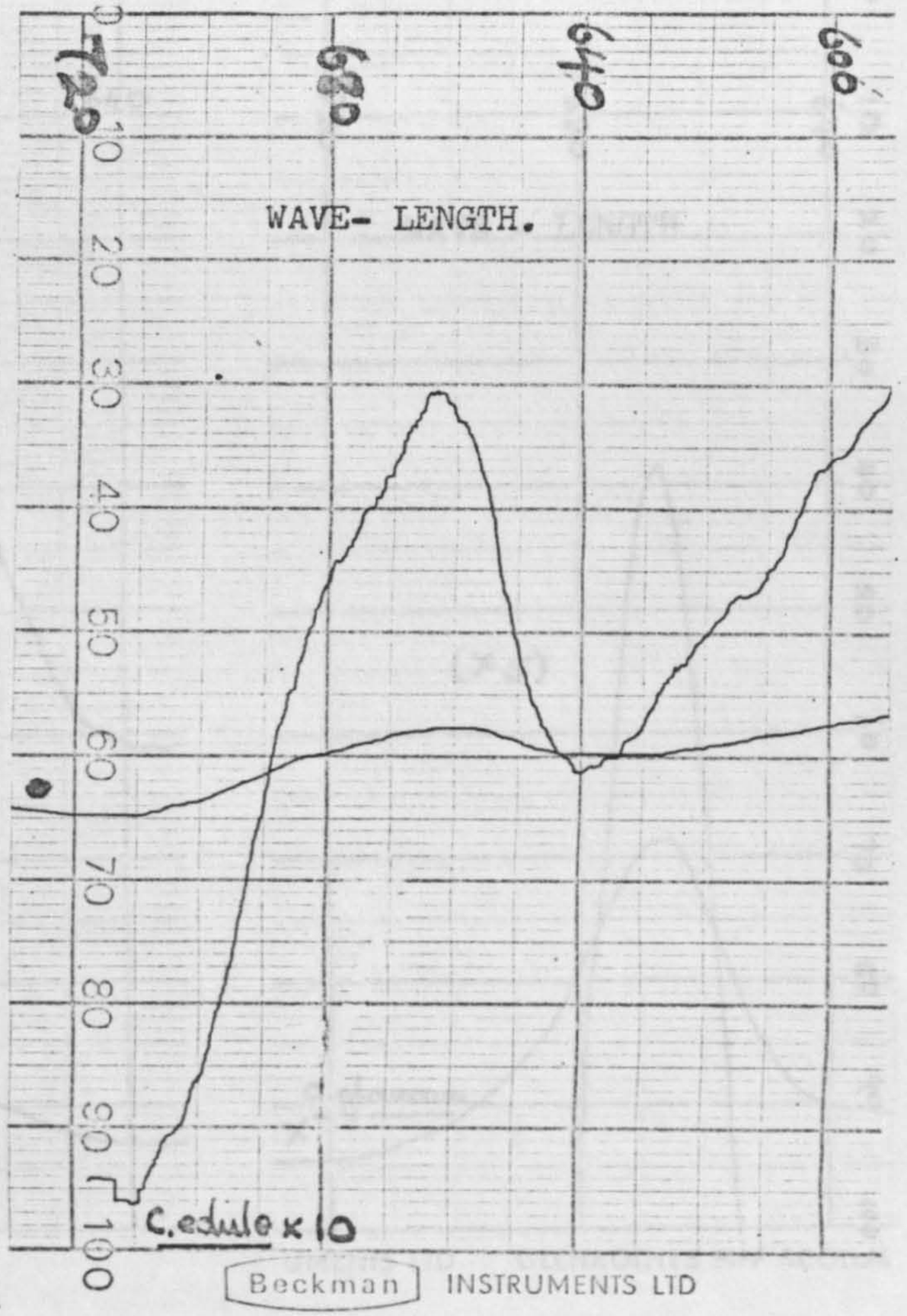


Fig 5 - Comparative absorption spectra of C.edule and C.glaucum collected on 22. 8.68. Examined on 25. 8.68 - after 3 days starvation in the laboratory. (scan of C. glaucum expanded in region of 700 nm to 540 nm.)

Scan of C. edule expanded (x10) in region between 710 to 590 nm's.

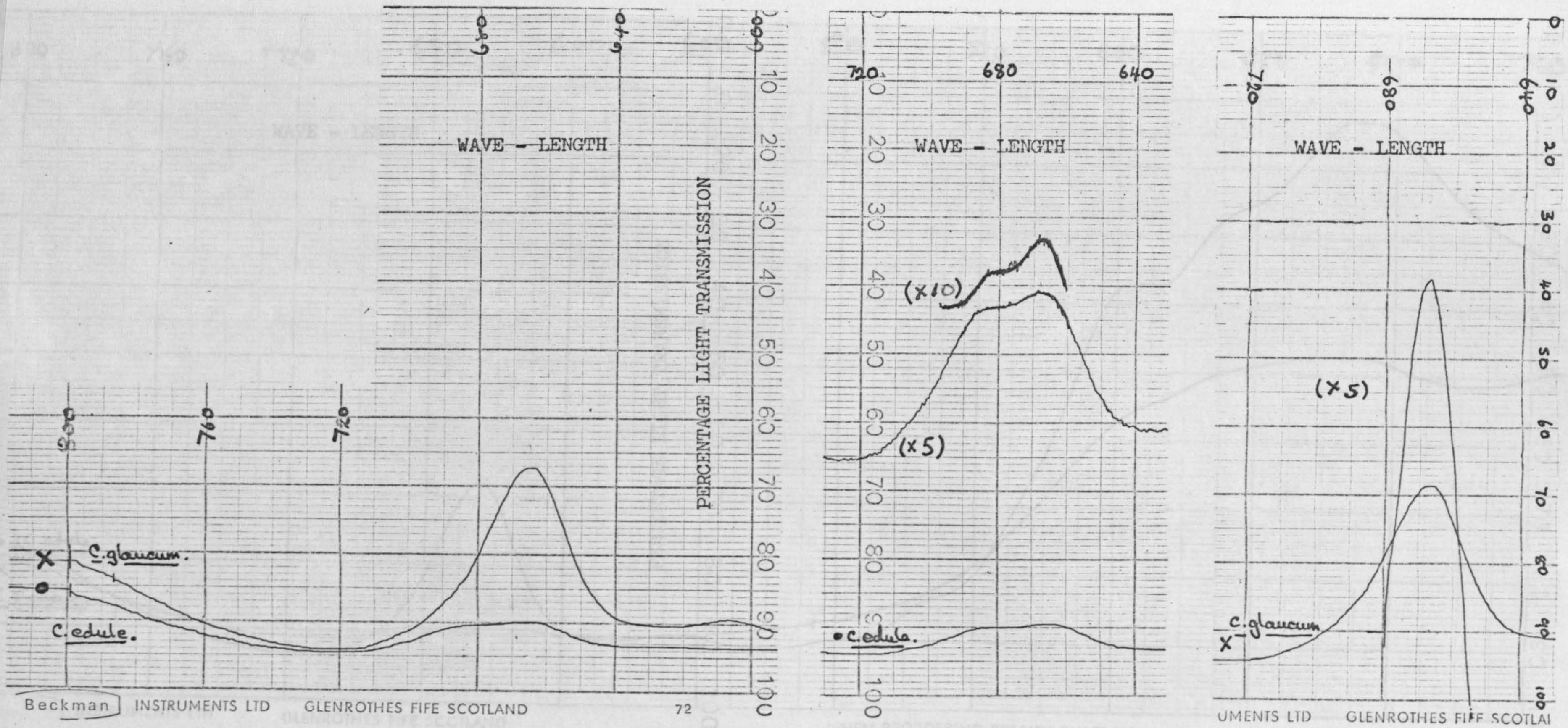


Fig 6 - Comparative spectra of C.edule and C.glaucum collected from the Crouch mixed cockle population on 22. 8.68. Extraction completed on 28.8.68. after 6 days starvation in the laboratory at 15°C. Both spectra have been expanded showing a double peak in C. edule and a single peak in C. glaucum.

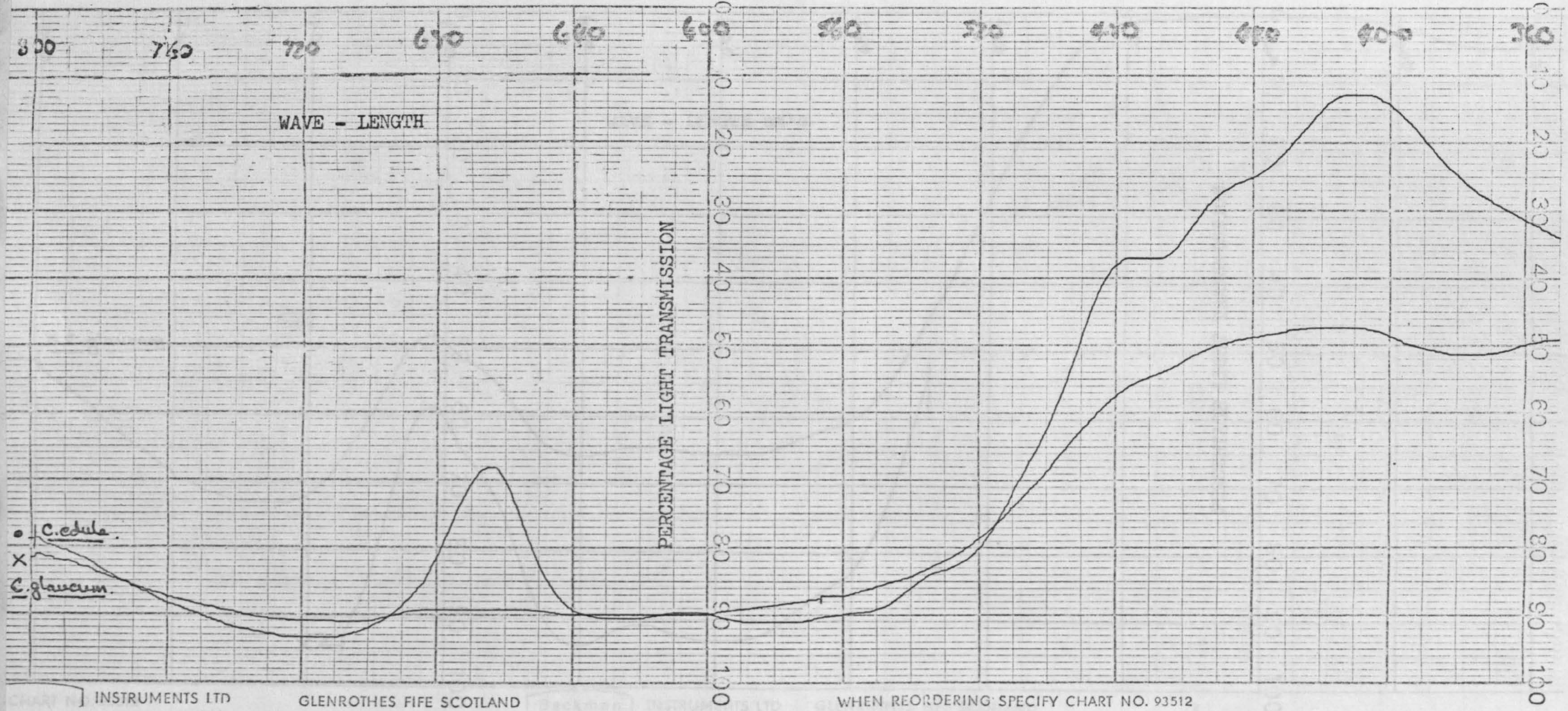


Fig 7 - Absorption spectra of acetone extracts of the digestive glands of C.edule and C.glaucum collected on the 22. 8.68 and examined after 22 days starvation on 13. 9.68.

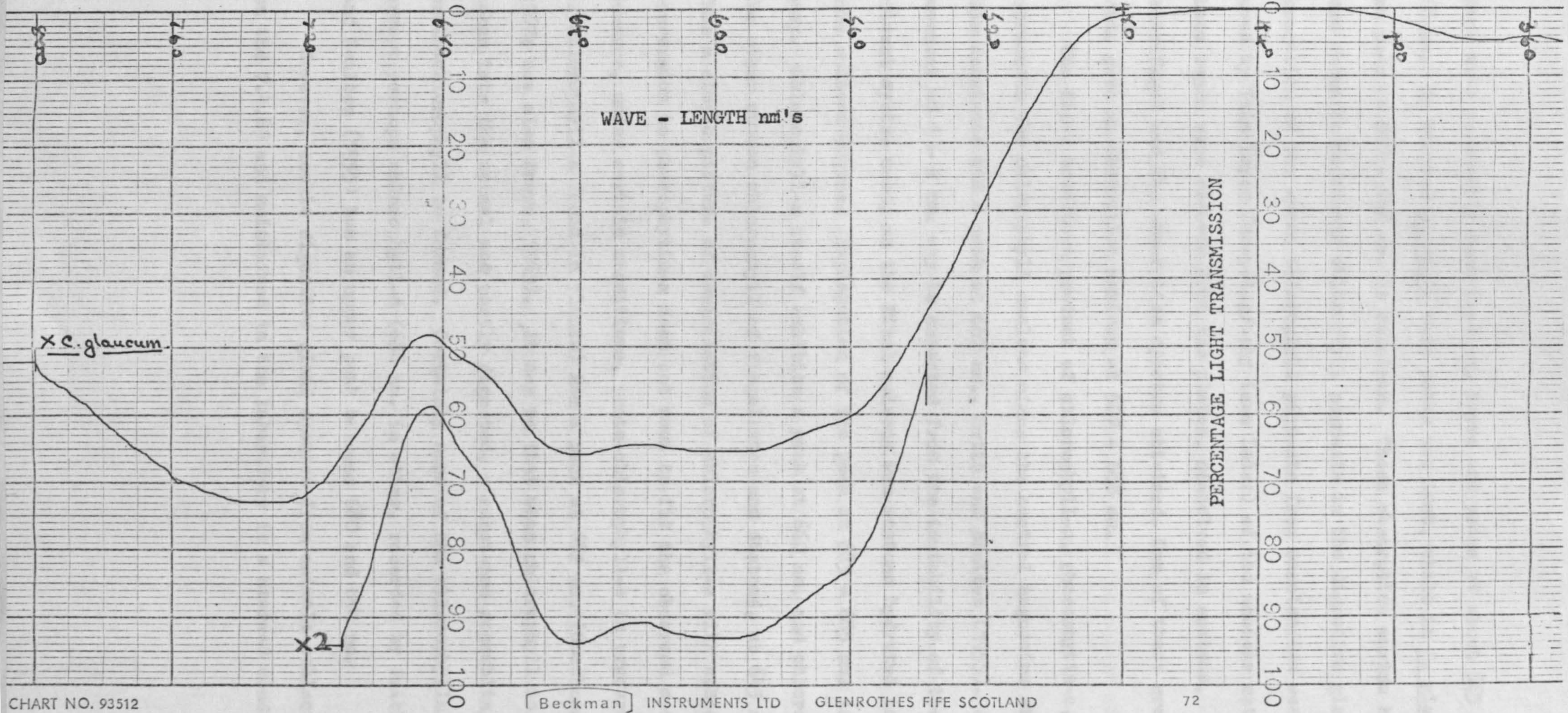


Fig 8 - Spectra of digestive gland of C. glaucum collected from Sheerness lagoon on 21. 9.68 examined immediately upon return to the laboratory.

which have presumably been feeding, there are peaks at about 685 and 668 nm. In starved C. edule both peaks are lost, while in C. glaucum one peak at 667 - 668 nm. is retained. These absorption maxima have been shown to represent chlorophyll pigments in the digestive gland. Separation of the green chlorophyll pigments from carotenoids was achieved by Thin-Layer Chromatography (see later) of the acetone extract. These bands were removed from the plates, dissolved in acetone, centrifuged and the absorption spectra obtained. One of these green bands gave an absorption maximum at 667 - 668 nm.

The first breakdown product of chlorophyll-a, phaeophytin-a, represents the chlorophyll nucleus minus the central magnesium atom. This substance has a peak at 667 nm., Smith and Benitez (1955). A movement of 1 - 2 nm. may be expected from the instability of the solvent system used, as the final solvent was acetone hydrated to some unknown degree. Explanation of the peak at 683 - 685 nm. is less easy. Chlorophyll-a itself exhibits a peak at 660 nm. and chlorophyll-b, the other common chlorophyll of flagellates and diatoms, at 643 nm. Thus a simple picture of assimilation of chlorophyll-a with subsequent conversion to phaeophytin-a does not seem to fit the observed spectra. However, under certain conditions, proto-chlorophyll-a (a precursor of chlorophyll-a found in plants) has a peak at 682 nm. (Goedheer, 1967; see also Brown, 1963). It may be that when chlorophyll is taken into the animal and partly digested, a substance resembling proto-chlorophyll is formed. Certainly none of the chlorophylls, except perhaps chlorophyll-d (688 nm. in ether, recorded by Smith and Benitez (1955) has an upper peak between 680 and 690 nm.

However, cockle digestive gland spectra from animals collected on the 7.4.69 and maintained in the laboratory in a starved condition

for 14 days, gave an identical picture in the two cockles (see fig. 9). Animals collected on the 22.4.69 and run on the 24.4.69 also gave the same scan pattern (see fig. 10). Thus it would seem that, in spring when flagellates and diatoms would be expected to be abundant, the pigments found in both cockles, examined straight from the shore in a starved condition, are very similar. The differences between the pigments in the digestive gland of C. edule in summer and spring may indicate a seasonal feeding difference in this cockle.

It would thus appear that the assumption that the colour of the digestive gland of C. edule was in some way correlated with food availability and type, has some basis in fact. The differences in the chlorophyll peaks in the acetone extracts of the glands of the two cockles in summer over a period of starvation, could well indicate that the digestion and breakdown of chloropyhll differs in the two cockles. In summer, the breakdown or removal of chlorophyll from the digestive gland is almost complete in C. edule after 3 days, whilst in C. glaucum the peak, thought to be phaeophytin-a, is maintained over a long period of time. The fact that the digestive gland of C. glaucum does not appear to undergo a seasonal change in size or colour, in contrast to the gland of C. edule, may be another example of a rhythm in a littoral animal which has been lost in a permanently submerged relative. Morton (1970) has shown that the digestive gland of C. edule exhibits a tidal rhythm in maintainance and secretion. It would be interesting to ascertain if any such rhythm is displayed by C. glaucum from littoral localities.

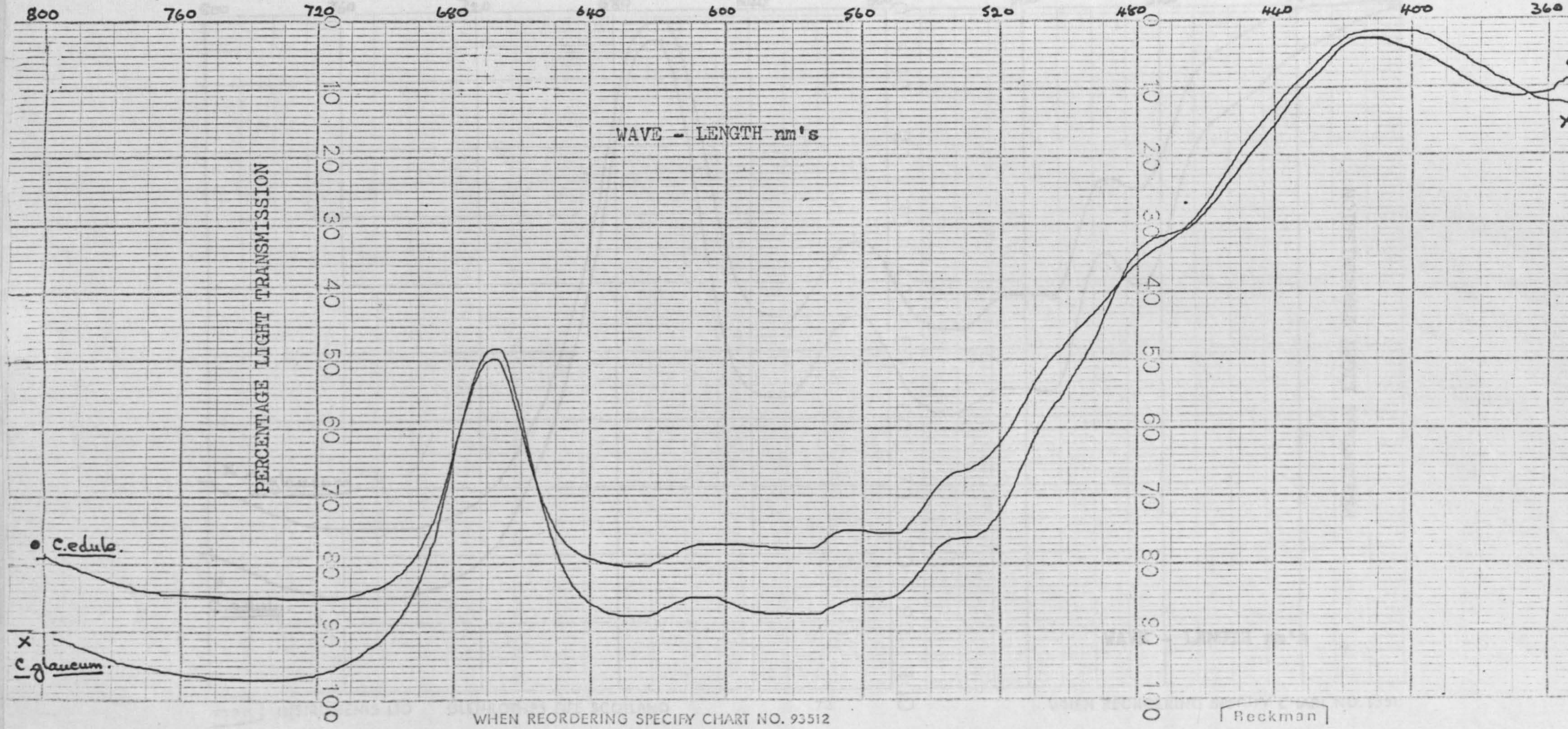


FIG 9 - Comparative spectra of C. edule and C. glaucum collected from the Crouch mixed cockle population on 7. 4.69 and maintained starved in the laboratory for 14 days.

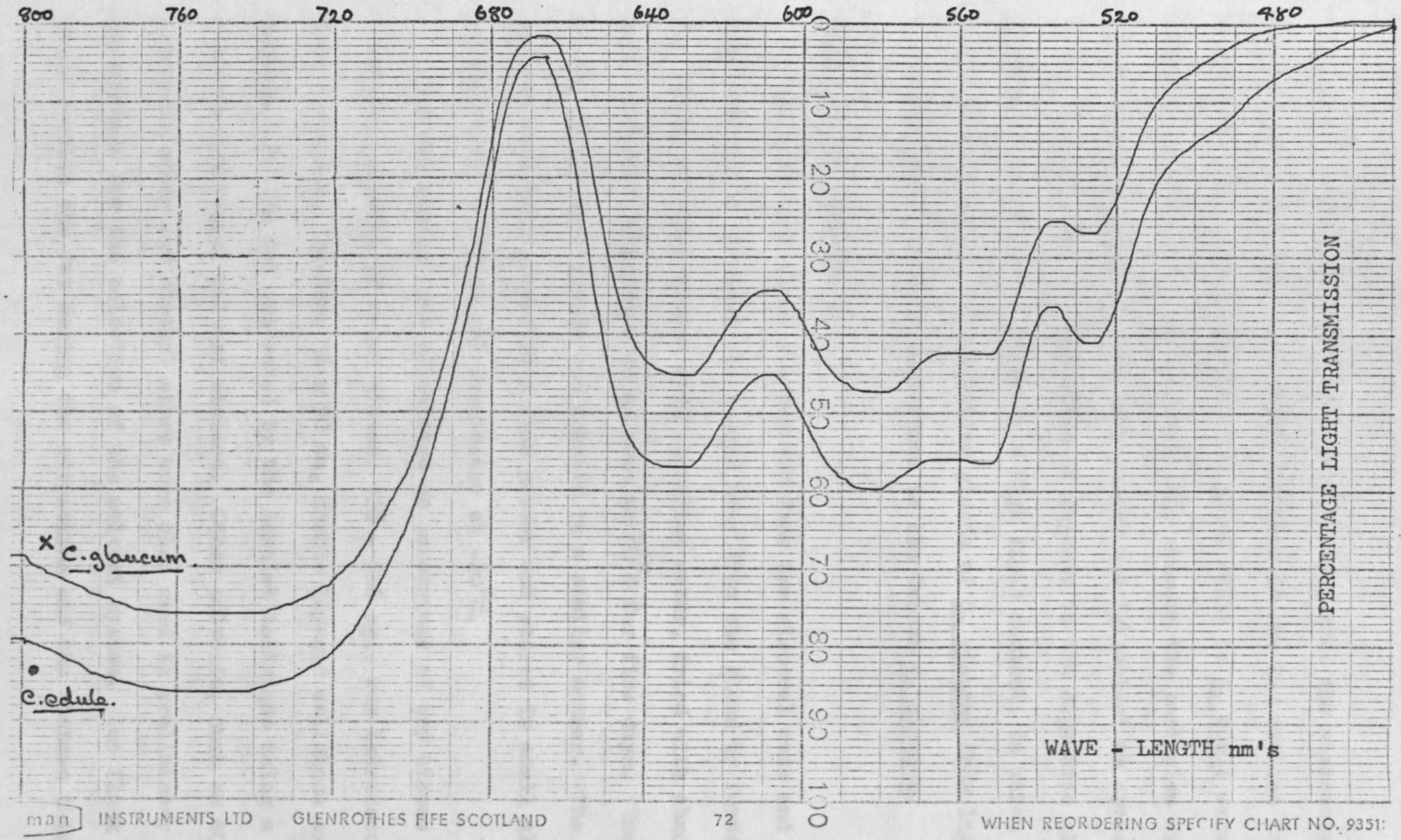


Fig 10 - Comparative spectra of cockles collected on 22. 4.69 and maintained starved in the laboratory for 48 hours before extraction.

2. Determination of the total fat content of the digestive glands of C. edule and C. glaucum.

It was noticed during the previous study that the microscopic appearance of the digestive gland differed in the two cockles from the common Crouch environment. The gland cells of C. edule were composed of very small brown particles, whereas the particles within the cells of C. glaucum were much larger and 'globular' in appearance. It was thought that the retention of pigment in the digestive gland of C. glaucum could be explained by a high lipid content, in which pigments would be dissolved. The digestive glands of C. glaucum from lagoon localities had a similar appearance to the Crouch C. glaucum.

Material and Methods.

The digestive gland was removed from the visceral mass and any gonad which was attached was teased away from the gland by forceps. The tissue was then washed with distilled water, dried with absorbent paper and then dehydrated in an oven at 80°C for five days. The remainder of the body tissue was treated in a similar manner. The dry tissues were then ground to a fine powder and stored in small glass phials within a silica gel dessicator at -20°C.

The fat content was calculated as percentage of dry tissue weight. A weighed quantity of dried tissue, 128 - 506 mg., was introduced into a Whatman, fat-free 10 x 50 cm, double layered cellulose extraction thimble, and the fat extracted by the Soxhlet technique using a 2:1 chloroform/methanol solvent mixture. Other solvents, such as 40/60° petroleum ether and diethyl ether were also used in preliminary experiments for the selection of the solvent system. The flask which would receive the fat during the extraction and the Whatman thimbles

were maintained before use in a dessicator.

Two semi-micro, quick-fit Soxhlet extraction apparatuses were used simultaneously, heating being supplied by electric mantles. A rate of reflux of about once every 3 - 5 minutes was maintained over a period of three hours, though most of the colour (consisting of carotenoidal impurities) was removed in the first four or five refluxes.

After extraction, the flask containing the solvent and fat was heated gently using the mantles, under reduced pressure. After removal of the solvent, the flask was placed in a dessicator and allowed to cool to room temperature before weighing. The quantity of fat was therefore determined by difference.

The tissues used in this analysis were obtained from cockles from the following localities:-

1. C. edule - 100 individuals C. glaucum - 75 individuals	LITTORAL	Collected on 11.1.69 from Hullbridge, River Crouch, Essex.
2. C. glaucum - 70 individuals	LAGOONAL	Collected on 29.1.69 from New England Creek, Essex.

Results and Discussion.

The values of chloroform/methanol extractable lipid calculated as percentage of dry weight are shown on table 1.

It can be seen, contrary to the predicted hypothesis that the digestive gland of C. glaucum was likely to contain more lipid than C. edule that the reverse was actually the case. The digestive gland of C. edule (20.9%) contains almost double the quantity of lipid found in C. glaucum (12.1%) from the same habitat in January 1969. The quantity found in the digestive gland and remaining tissues of

Table 1 - Percentage lipid content of the digestive gland and remaining tissues of the Crouch Cerastoderma in January 1969.

Cerastoderma edule				Cerastoderma glaucum			
Digestive gland		Remaining tissues		Digestive gland		Remaining tissues	
Dry weight of sample(mgs)	Percentage Lipid	Dry weight of sample(mgs)	Percentage Lipid	Dry weight of sample(mgs)	Percentage Lipid	Dry weight of sample(mgs)	Percentage Lipid
150.9 "	21.9%	238.3 "	11.7%	305.4 "	12.6%	177.9 "	12.8%
207.7 "	22.5 "	269.3 "	9.4 "	198.1 "	12.3 "	329.6 "	12.8 "
312.1 "	18.7 "	126.2 "	11.1 "	277.6 "	11.5 "	370.3 "	11.7 "
445.0 "	20.7 "	257.0 "	8.8 "	177.4 "	11.9 "	181.7 "	11.7 "
400.0 "	21.5 "	284.0 "	10.8 "	326.9 "	12.1 "	253.5 "	12.0 "
250.0 "	20.5 "	251.2 "	12.4 "	289.9 "	12.4 "	-	-
-	-	494.5 "	11.6 "	-	-	-	-
-	-	393.7 "	9.2 "	-	-	-	-
-	-	253.6 "	10.7 "	-	-	-	-
-	-	321.7 "	10.5 "	-	-	-	-
-	-	201.9 "	10.9 "	-	-	-	-
-	-	506.3 "	10.3 "	-	-	-	-
Mean of 6 values:-	20.9%	Mean of 12 values:-	10.6%	Mean of 6 values:-	12.1%	Mean of 5 values:-	12.2%
Range:	18.7 - 22.5 (3.8 %)	Range:	8.8 - 12.4 (3.6 %)	Range:	11.6 - 12.6 (1.1 %)	Range:	11.7 - 12.8 (1.1 %)

C. glaucum (12.1 and 12.2%) was very similar indeed and a little above that found in the remaining tissues of C. edule (10.6%). Even though the percentage lipid content of the C. edule gland was higher than that found in C. glaucum, the absolute quantities in each gland may well be similar, as it has previously been shown that, in winter, the gland is larger in C. glaucum.

The scatter recorded in the percentage values is probably due to the fact that the tissues were ground into a powder and then sampled. Although this technique is considered to be 'not the most satisfactory method' by Barnes and Finlayson (1963) and Giese (1967), in comparative experiments, because of its relative ease to undertake as regards time and apparatus, it has some value. Another reason for the scatter could well be the gonad condition of the cockles. In winter, the majority of C. glaucum are indeterminate (82%) - see section VI, whilst only 46% of C. edule are in this condition. The remaining 54% show a variety of gonad developmental stages and this could well explain the less uniform tissue values of C. edule in contrast to C. glaucum.

The values obtained for the lagoon C. glaucum are shown overleaf and from these it can be seen that C. glaucum from a lagoon locality contained less lipid in the digestive gland compared with C. glaucum from a littoral location. In fact, a slightly higher value was found in the remaining body tissues compared with the digestive gland. This could be regarded as evidence that the lagoon cockles have less food available than the littoral cockles.

Spector (1963) records Cardium corbis, a Canadian east-coast cockle, as containing only 2.7% lipid. However, Giese and Hart (1967) determined the lipid content (more precisely the chloroform/methanol

Percentage lipid content of the digestive gland and remaining tissues of Cerastoderma glaucum from New England Creek, Essex.

Digestive Gland		Remaining Tissue	
Dry weight of sample (mgs)	Percentage lipid	Dry weight of sample (mgs)	Percentage lipid
492.7	7.5 %	440.2	9.2 %
632.0	8.4 %	205.7	9.6 %
421.0	8.2 %	306.9	9.3 %
Mean value	8.01%		9.36%

extractable material, as has been determined above) of various tissues of the chiton, Katharina tunicata. The digestive gland percentage varied from 11 to 20% through a yearly cycle. The average value obtained, 13.6% dry weight, compares favourably with those obtained for C. glaucum. The majority of the remaining tissues of the chiton contained less lipid material. The lamellibranch Trivela stultorum has been shown to contain 14.1% lipid in the digestive gland (Giese, Hart, Smith and Cheung, 1967) whilst the lobster Panulirus polyphagus is recorded to contain 10.72 - 30.6% lipid in this gland (George and Patel, 1956). For a more complete survey of lipid content of various invertebrates see Giese, 1969. It would seem, therefore, that the values obtained for C. edule and C. glaucum in this survey are, in general, comparable with those recorded in the literature.

In summary, in winter it has been shown that the percentage lipid content per unit dry weight is greater by a factor of approximately 2 in C. edule compared with C. glaucum from the same environment.

3. Thin - layer chromatography of the digestive gland lipids of Cerastoderma edule and Cerastoderma glaucum from the Crouch mixed population.

It has been shown earlier that during the winter months the percentage of solvent extractable material from the digestive gland of C. edule was almost double that found in C. glaucum. As most of this material is lipid, thin - layer chromatography of the lipid constituents of the digestive glands was conducted, to determine whether the same main lipid classes were found in both cockles. As the differences had also been detected in the spectrophotometric extracts of the glands of the two cockles associated with starvation in the laboratory, cockles were maintained in filtered water for periods of time and then chromatography of the lipids conducted.

The application of Thin - Layer Chromatography (T.L.C.) to the separation of lipids is well documented, (Mangold, 1961, 1965; Randerath, 1963; Padley, 1964; Smith and Stevens, 1969). Lipids are a group of compounds varying from highly polar forms, such as phospholipids, to non-polar triglycerides and sterol esters. Between these extremes are a variety of classes which exhibit varying degrees of polarity. For this reason, by using an appropriate solvent system, they are separable by T.L.C. A relatively polar solvent, e.g. petroleum ether/ diethyl ether/acetic acid (84:15:1) distributes the non-polar elements of the lipid extract (the neutral lipids) on the absorbent plate, whilst by using a strongly elutive solvent, e.g. chloroform/methanol/ water (65:30:5), the non-polar elements run with the solvent front and the polar phospholipids then become distributed upon the plate.

Lipids are generally unsaturated compounds and can easily be

made visible after chromatography by spraying the plate with 1% iodine in methanol solution. The lipids appear as brown spots on a slightly yellow background. Some saturated lipids and esters are also made visible by this technique (Sunderath, 1963).

Material and Methods.

Cockles of both types were collected on 8.12.68 from the Crouch mixed population and maintained at 5°C in filtered, aerated, regularly changed sea-water. The digestive glands were removed from several individuals, washed in distilled water and then either treated as wet tissue or dried in an oven at 80°C for 72 hours. As will be shown, there did not appear to be any difference between the lipid classes found in wet and dry tissue. The dry tissue was ground to a fine powder and maintained in a dessicator at -20°C before use.

The lipids were extracted following the method of Blank et al. (1964). About 50mg. of dry tissue (or approximately 0.6gms of wet tissue) was ground in a glass tissue grinder, with, initially, 1.5 mls. of chloroform/methanol (2:1) and then further treated with 1ml. and 2 mls. of the solvent mixture. The solutions from the extraction were then combined, centrifuged, filtered through celite-454 and finally the supernatant evaporated to dryness. The fatty residue was then successively dissolved in diethyl ether and petroleum ether (40/60°C), with drying between to remove any water. To the residue was then added 0.5 ml. of petroleum ether which was then applied to thin-layer plates. For the phospholipid study the final solvent used was chloroform/methanol (1:1). 20 x 20 cm. sized plates were coated with 250 μ silica gel G with binder using a Shandon Unoplan Leveller, Model 'P'. The plates were left horizontal for 4 minutes at 110°C

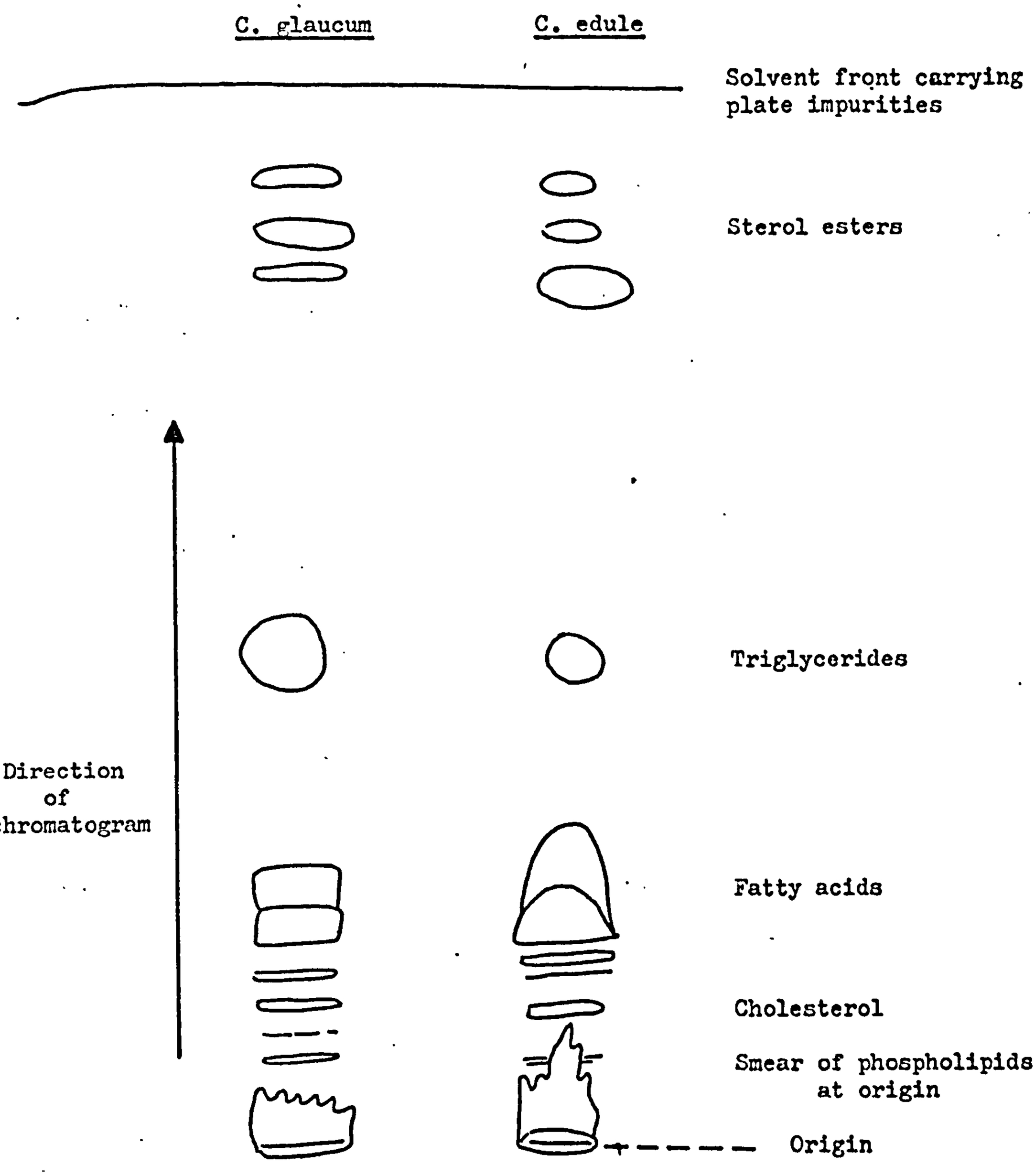
and then for a further 20 minutes vertical at the same temperature. They were maintained in a desiccating chamber. Immediately prior to use, the plates were re-heated to 110°C for 15 minutes to activate and then cooled before ap lication of the lipid carrying solvent.

At least six hours before the chromatography run, the selected solvent system, e.g. petroleum ether/diethyl ether/acetic acid (85:15:1) was introduced into the Universal T.L.C. Chromotank. Filter papers, dipping into the solvent, were placed on the inside surfaces of the tank, to saturate the tank atmosphere.

The lipid solvent extract was added to the plate in small streaks from a graduated micro-pipette. In all comparative runs between the two cockles, equal quantities of digestive gland extract were added to the streaks on the same plate. The plates were developed in the dark for about 20 minutes vertically at room temperature. After the solvent front had travelled approximately 16-17 cms. the plates were removed from the tank, dried in the air for 15 minutes and the lipid spots were then made visible by spraying with 1% solution of iodine in methanol.

Results.

It can be seen from the distribution of non-polar lipids shown on fig. 11 and plate 2, that the wet digestive gland extracts examined immediately after collection from the shore on the 8.12.68, are very similar in the two cockle types. Likewise, the distribution of neutral lipids from the dry tissue extracts shown on plate 3, are similar to those obtained for the wet tissues. By reference to standards, the main lipid classes could be determined and these have been placed on fig. 11. Thus it would seem that heating at 80°C for three days does not alter the neutral lipid composition of the digestive gland extracts.



Solvent system - Petroleum ether/ diethyl ether/ acetic acid(84:15:1)

Dry tissue weights: C.glaucum - 0.0455 gms.
C.edule - 0.0449 "

Plate - 250u activated silica gel G

Detection - 0.1 % iodine in methanol

Date of run - 18.12.68.

Fig 11 - Plan of typical comparative chromatogram of the non - polar lipids of C. edule and C. glaucum showing the distribution of the main lipid classes.

Plates 2 & 3 - Thin - Layer Chromatography of neutral lipids extracted from the digestive glands of C. edule and C. glaucum. Cockles examined immediately after collection.

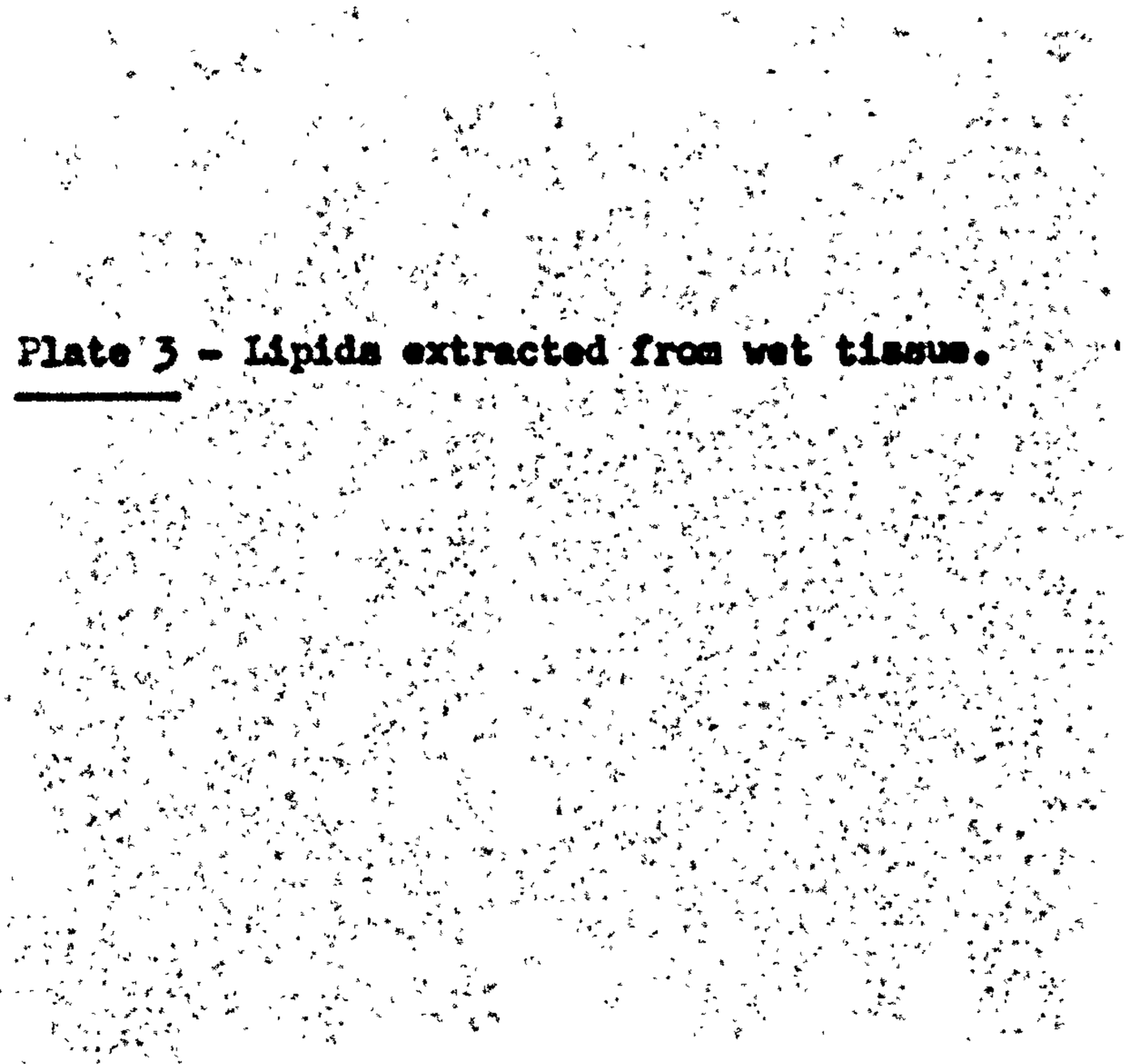
Plate 2 - Lipids extracted from dried tissue.

E G E G E G E G E G E

E = C. edule

G = C. glaucum

Plate 3 - Lipids extracted from wet tissue.



G E G E G E G E

Plate 2

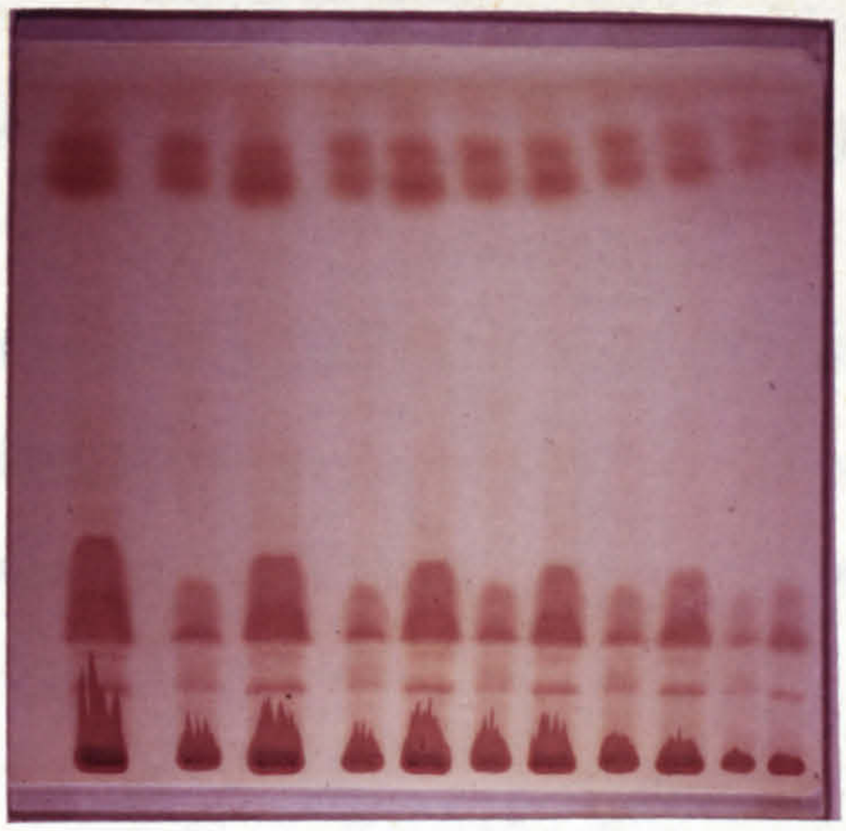
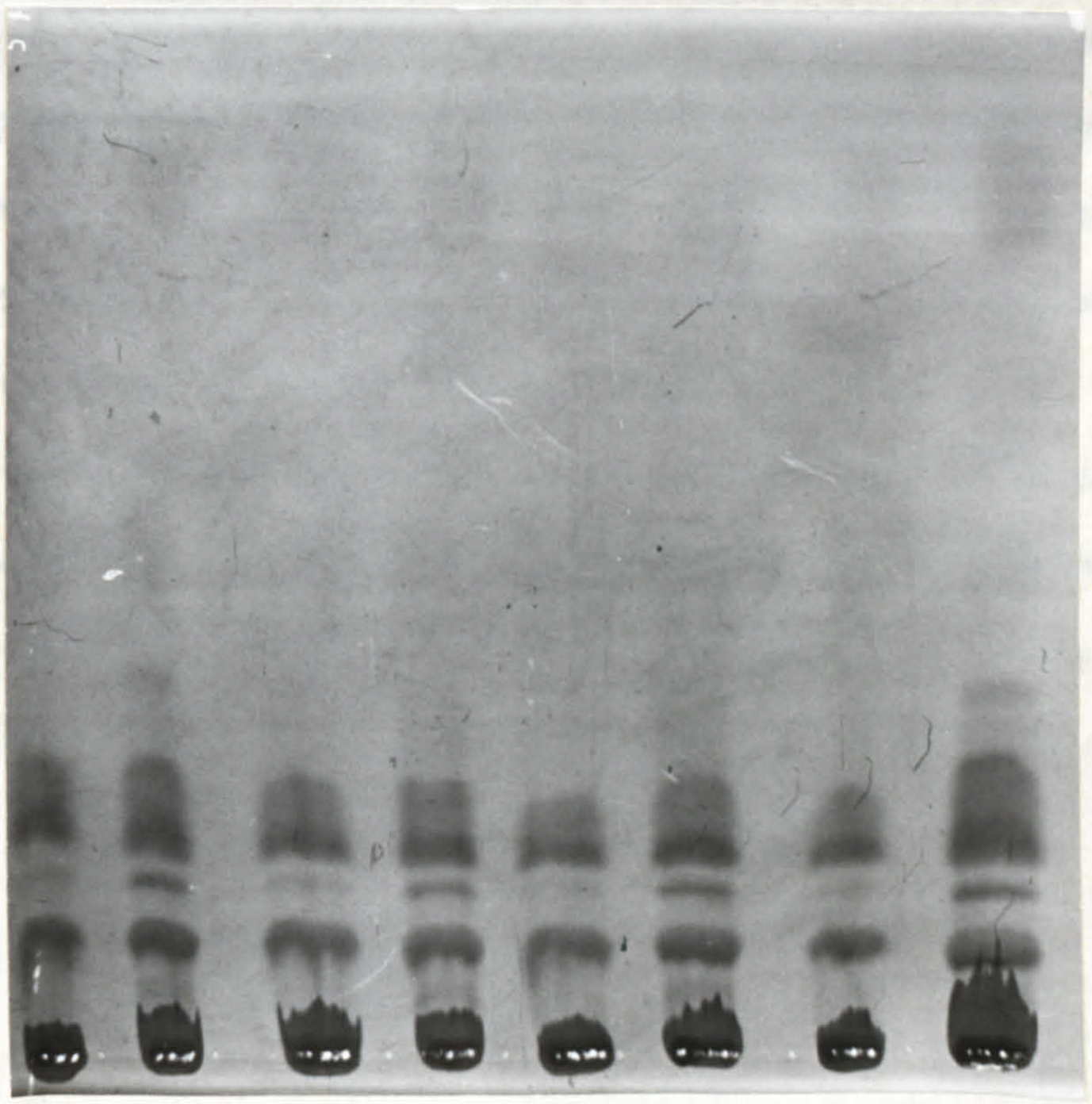


Plate 3



The cockles were maintained in the laboratory for 12 days until 20.12.68 and the chromatograms obtained of the non-polar lipids from the digestive glands of the two cockles are shown on plate 4. For an equal quantity of digestive gland, the majority of the triglyceride and fatty acid components appears to be lost from C. glaucum in contrast to C. edule.

Using the non-polar solvent, chloroform/methanol/water (63:30:5), (Randerath, 1963), the distribution of phospholipids obtained, (see fig. 12) was also similar in the two cockles. The chromatograms of phospholipids from the digestive gland were identical in the two cockles, before and after starvation for four weeks. Thus, the polar lipid element of the digestive gland did not alter with starvation. In a comparative investigation of lipids in free-living infective larvae and parasitic adult nematodes, Barrett (1968) found no difference in the phospholipid content in the different stages, but did note a difference in the neutral lipids. He found that free fatty acids were the principle component of the neutral lipid fraction of the infective larval nematodes, but that in the parasitic adults, triglycerides formed a much larger percentage of the total neutral lipids. It would appear that the fatty acids and triglycerides of animals are far more variable and environmentally determined than the polar lipids. On the other hand, phospholipids are very much more stable than neutral lipids and an identical picture was even found in the two closely related cockles.

Thus, in this quantitative examination, the phospholipid constituents of the digestive glands of C. edule and C. glaucum appeared to be the same before and after starvation. The same main neutral lipid classes were also found in both cockles before starvation, but after

Plate 4 - Thin - Layer Chromatography of neutral lipids extracted from the digestive glands of cockles starved for 12 days.

E G E G E G E G E G

E = C. edule

G = C. glaucum

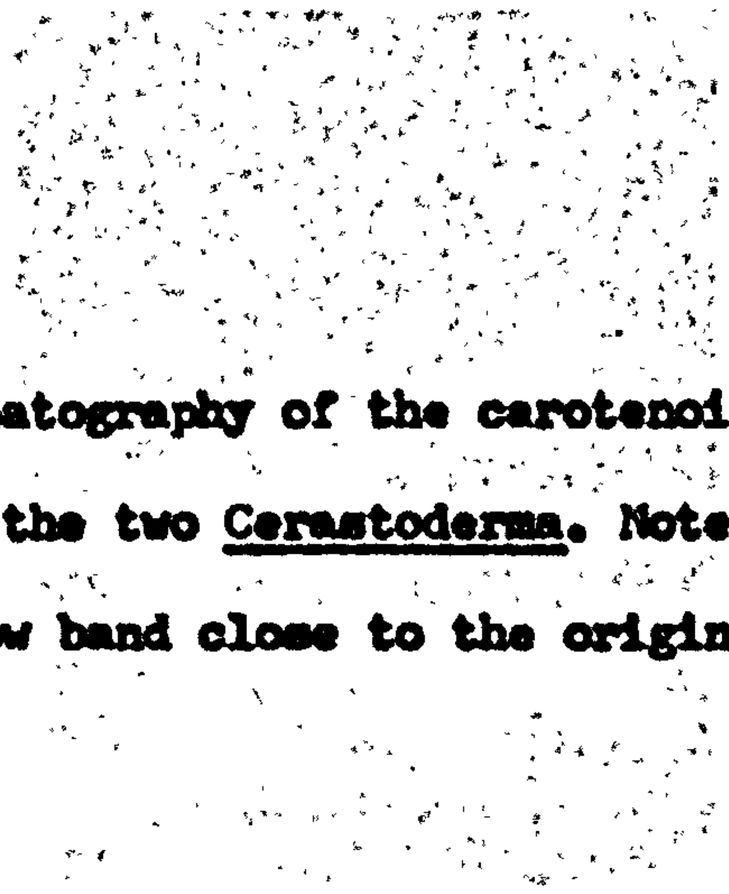


Plate 5 - Chromatography of the carotenoids extracted from the two Cerastoderma. Note the very polar yellow band close to the origin.

C. GLAUCUM C. EDULE

Plate 4

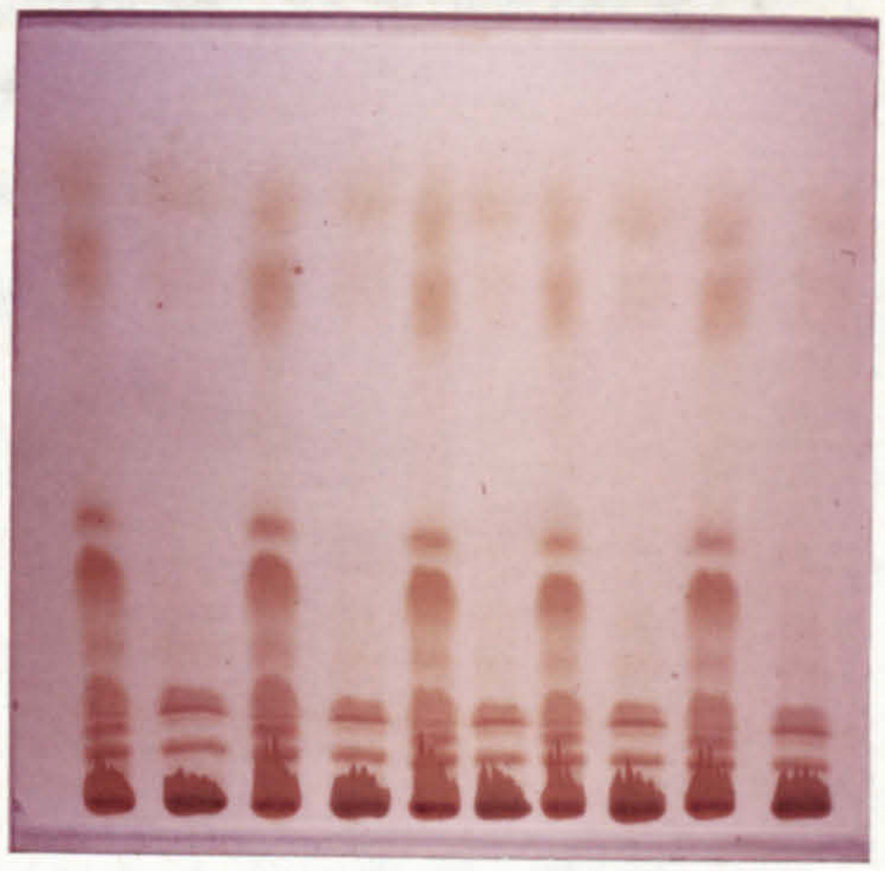


Plate 5

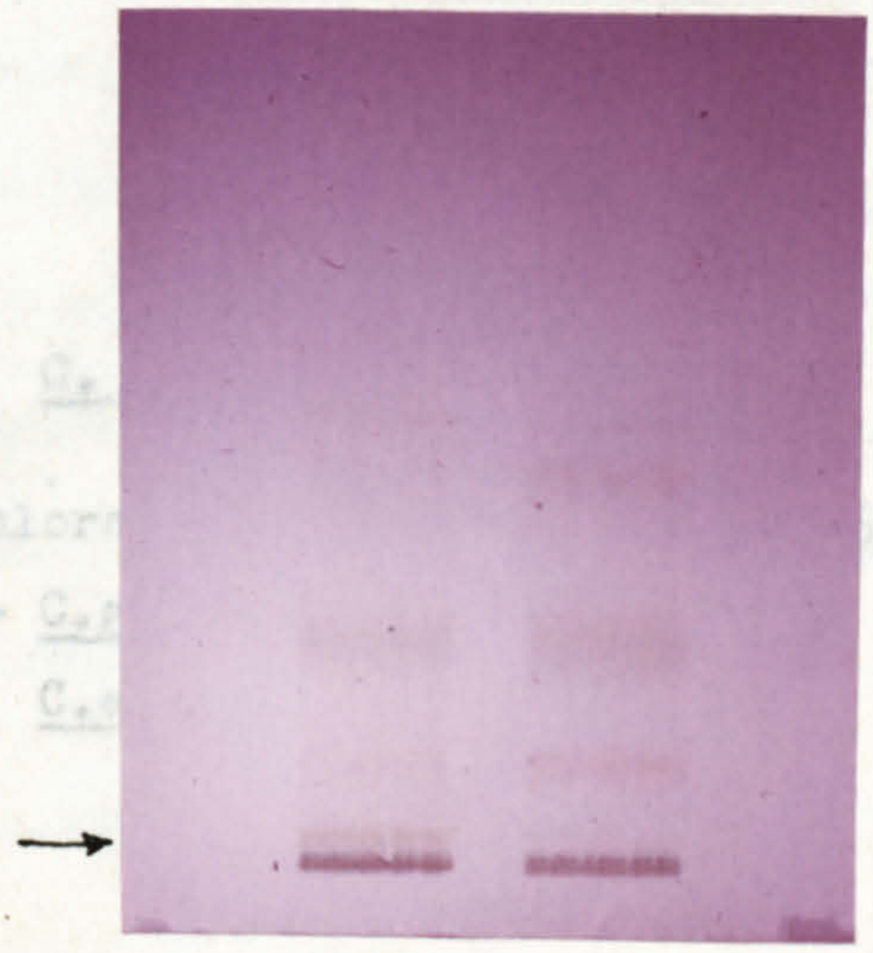
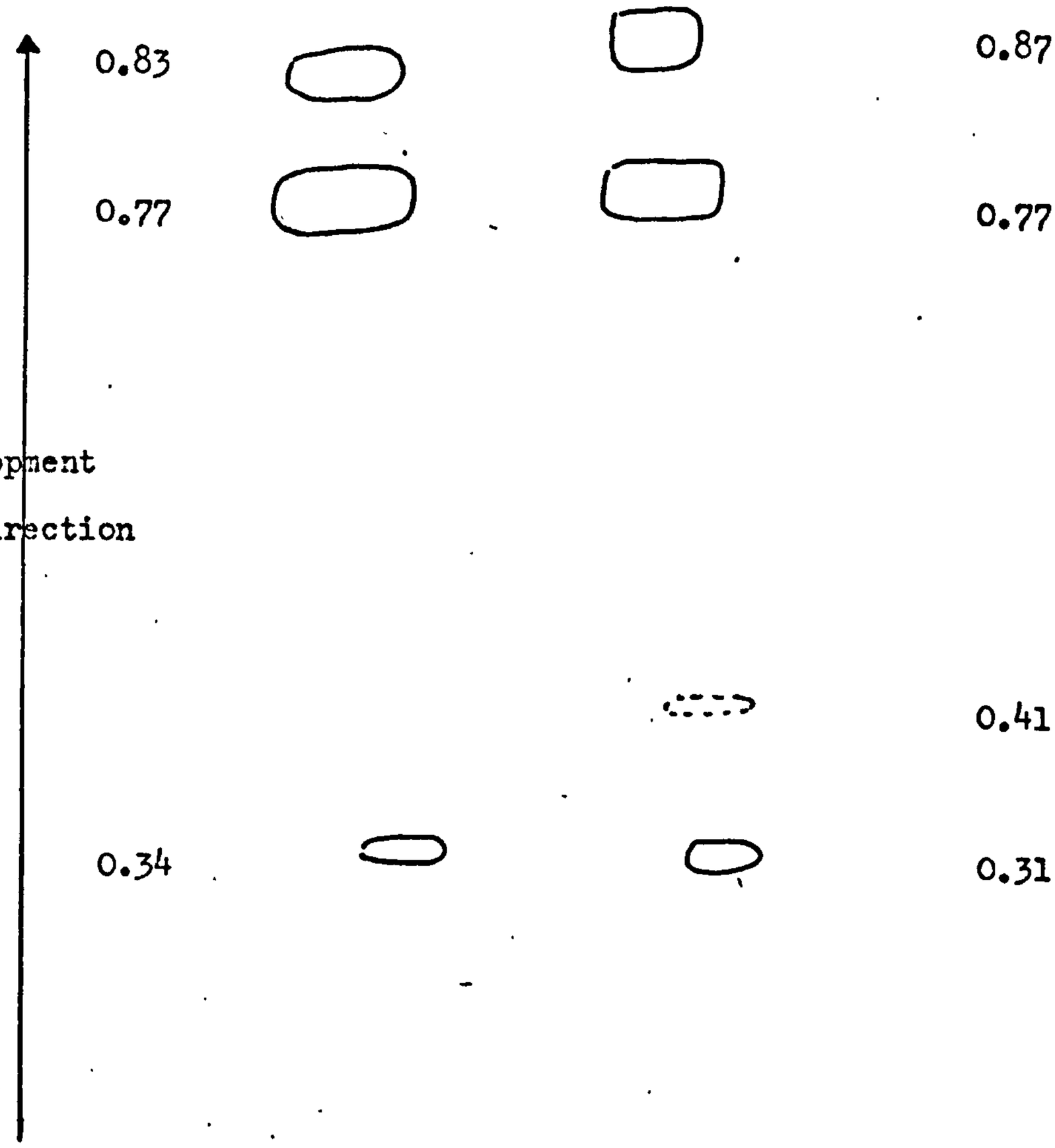


Fig 12 - Comparative chromatograms showing distribution of phospholipids as separated by T.L.C. of *C.edule* and *C.glaucum*.

Solvent front

R. f. factors

R. f. factors



Origin

C. glaucum C. edule

Solvent system - Chloroform/ methanol/ water (65:30:5)

Dry tissue weight - C.glaucum - 0.041 gms.

C.edule - 0.039 "

Fig 12 - Comparative chromatograms showing distribution of phospholipids as separated by T.L.C. of C.edule and C.glaucum.

a period of starvation, the triglyceride and fatty acid components of the digestive gland were lost from C. glaucum but retained in C. edule.

4. Separation of carotenoid pigments from the digestive glands of C. edile and C. glaucum.

Chromatographic methods, initially paper, but more recently thin layer and electrophoresis, have been used in taxonomic studies to separate closely related animals. Buzzati-Traverso and Rechnitzer (1953), Fox (1956) and Porter (1964), have employed paper chromatographic techniques, but these methods have been superceeded by electrophoresis of tissue extracts, (Connell, 1953a,b; Sibley, 1960; Manwell and Baker, 1963; Wilson and Kaplan, 1964; Leone, 1964; Manwell, 1966; Manwell and Kerst, 1966; Manwell et al., 1967; Reid and Dunnil, 1969).

The carotenoids of organisms have been studied to throw light on phylogenetic relationships. Dales (1960) examined the pigments of various Chrysophycean flagellates from a taxonomic viewpoint and the carotenoids of Mytilus edulis and Mytilus californianus have been examined by Campbell (1968), who showed that the English and American mussels contained the same range of carotenoids, differing only in the concentration of the separate carotenoid constituents.

The separation of cockle carotenoids has been undertaken here by Thin-Layer Chromatographic (T.L.C.) techniques. The investigation into these pigments of the digestive glands of the two cockles C. edule and C. glaucum is reported below.

Material and Methods.

Both cockle types were collected from the Crouch mixed cockle population on 7.4.69, unless otherwise stated.

Technique for separation of carotenoids.

T.L.C. - see previous section.

Absorbent.

20 x 20 cm., 250 μ thick plates of silica gel G according to stahl (= kieselguhr G nach stahl), were produced as previously. They were pre-run in methanol to remove gel impurities (polytheres?) (see Galasko, 1970), the impurities running with the solvent front. The plates were then reactivated for 40 minutes at 110°C.

Methods of extraction.

The wet digestive gland was washed with distilled water and then ground in a glass tissue grinder, the pigments being extracted with 9 - 10 mls. of acetone. After extraction, the acetone solution was centrifuged and filtered through celite - 454, as previously. The combined extracts were then concentrated under vacuum by rotatory evaporation. Benzene was added to the crude carotenoidal/lipid extract, forming an azeotropic mixture with water. The water was removed by further evaporation of this mixture and the final extract was maintained under nitrogen in the dark at -20°C. A small quantity of petroleum ether or benzene was added to dissolve the extract prior to plating.

Solvent systems.

(1) Mixture of Acetone/Petroleum ether (25:75 or 40:60).

(2) Petroleum ether (60°/80°C)/Acetone/Methanol (60:35:5).

(3) Chloroform/Methanol/Water (65:30:5).

Chromatographic run.

The chromatographic tanks were usually flushed with nitrogen and then always left for at least one hour after addition of the solvent system to ensure complete tank saturation. Ascending runs were completed in the dark at room temperature (17 - 21°C), for approximately 15 - 20 cms.

Detection.

As most carotenoids are coloured, their presence on the plate is visible during the chromatographic run and thus no special method of detection is required. The plates were examined immediately upon termination of the run (as xanthophylls in particular are converted into colourless products by oxidation) and the distribution of carotenoid fractions noted. A single very polar carotenoid, which was immediately noted as being of interest, was removed from the plate, eluted in an appropriate solvent and the absorption maxima (λ max.) determined using either a D.B.Beckman or a Unicam S.P.700 recording spectrophotometer.

A larger quantity of acetone extractable material was obtained from the digestive glands of 45 C.glaucum collected from Gosport lagoon on 6.6.69. This was chromatographed on large 50 x 40 cm. plates using kieselguhr H as the absorbent. These plates had previously been run in methanol and re-activated as before. The polar carotenoid fraction of these plates, mentioned above, was investigated in an attempt to elucidate its structure (see later).

Results.

The distribution of carotenoids on the plates varies with the polarity of the solvent system used and with the activity of the plate. Thus, the recording of R_f values is of little value apart from indicating the general polarity of the carotenoids, unless there is direct comparison with standards. Unfortunately, few such standards were available in this study. The effect of the polarity of the solvent upon separation of the chlorophylls and carotenoids is shown on fig. 13. Clearly, The non-polar solvent system based upon petroleum ether is suitable for separation of carotenoids. For the remainder of the chromatographic runs, 40% acetone/60% petroleum ether or 25:75% petroleum ether was selected.

In the spring and early summer, when this survey was undertaken, the colour of the digestive gland of the two cockles appeared quite similar (C. glaucum was black, while the gland was dark green in C. edule). The distribution of carotenoid from these digestive glands is shown on fig. 14. Essentially, one very polar xanthophyll was very prominent in C. glaucum, whereas in C. edule it was present on the thin-layer plate in only trace quantities (see plate 5).

Animals which had been maintained in the laboratory for two weeks (collected 7.4.69) were compared on 20.4.69. Equal quantities of wet tissue from both cockle types was extracted with acetone and compared using a 40:60 acetone/petroleum ether solvent system. It can be seen in fig. 15 that the difference in extractable carotenoids was retained in starved animals. Cockles which had been maintained in filtered water until the 2.5.69 (a total of 25 days) also showed this difference (see fig. 16). Thus from the taxonomic point of view, the carotenoid

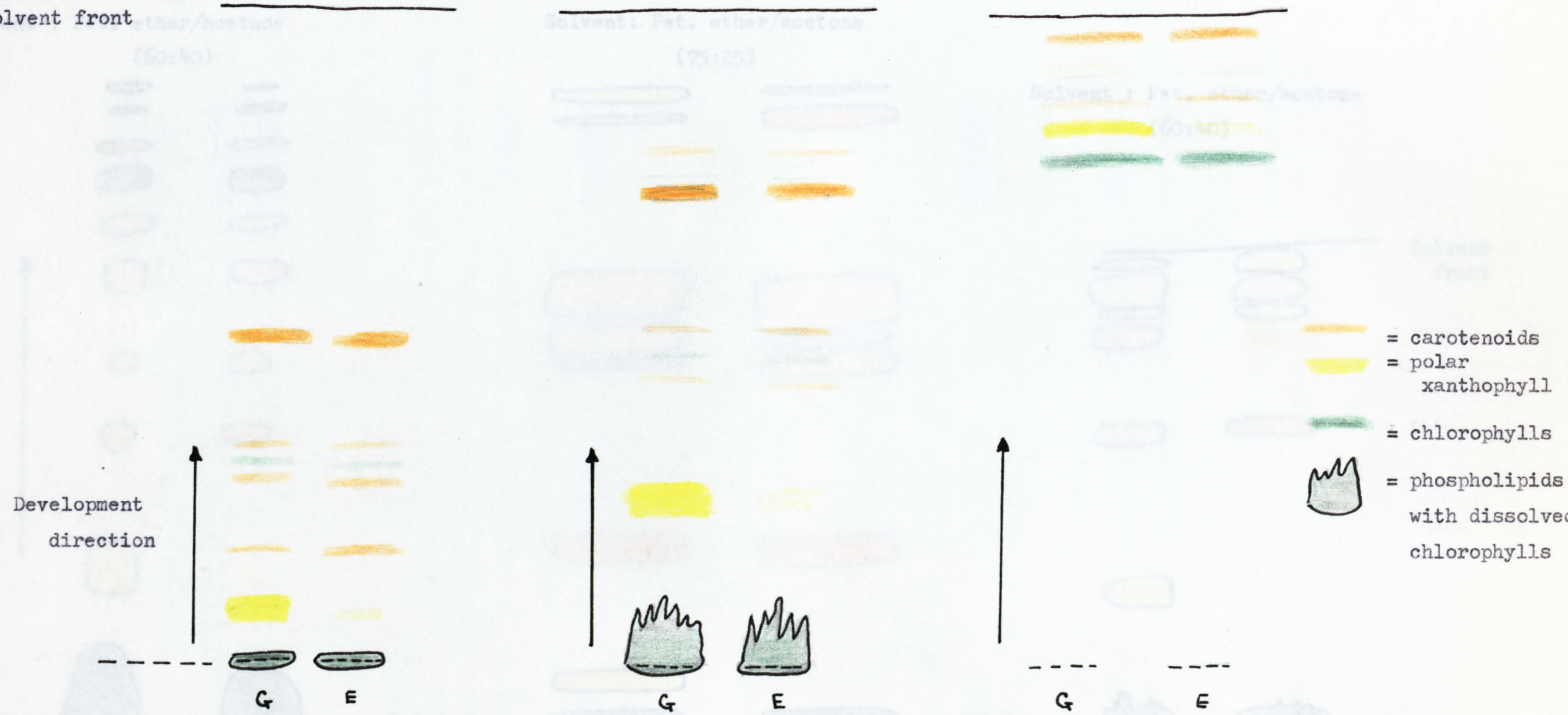


Fig 13 - Comparative T.L.C. of the acetone extracts of the digestive glands of C.edule(E) and C.glaucum(G) showing the effect of solvent polarity upon the separation of the carotenoids and chlorophylls.

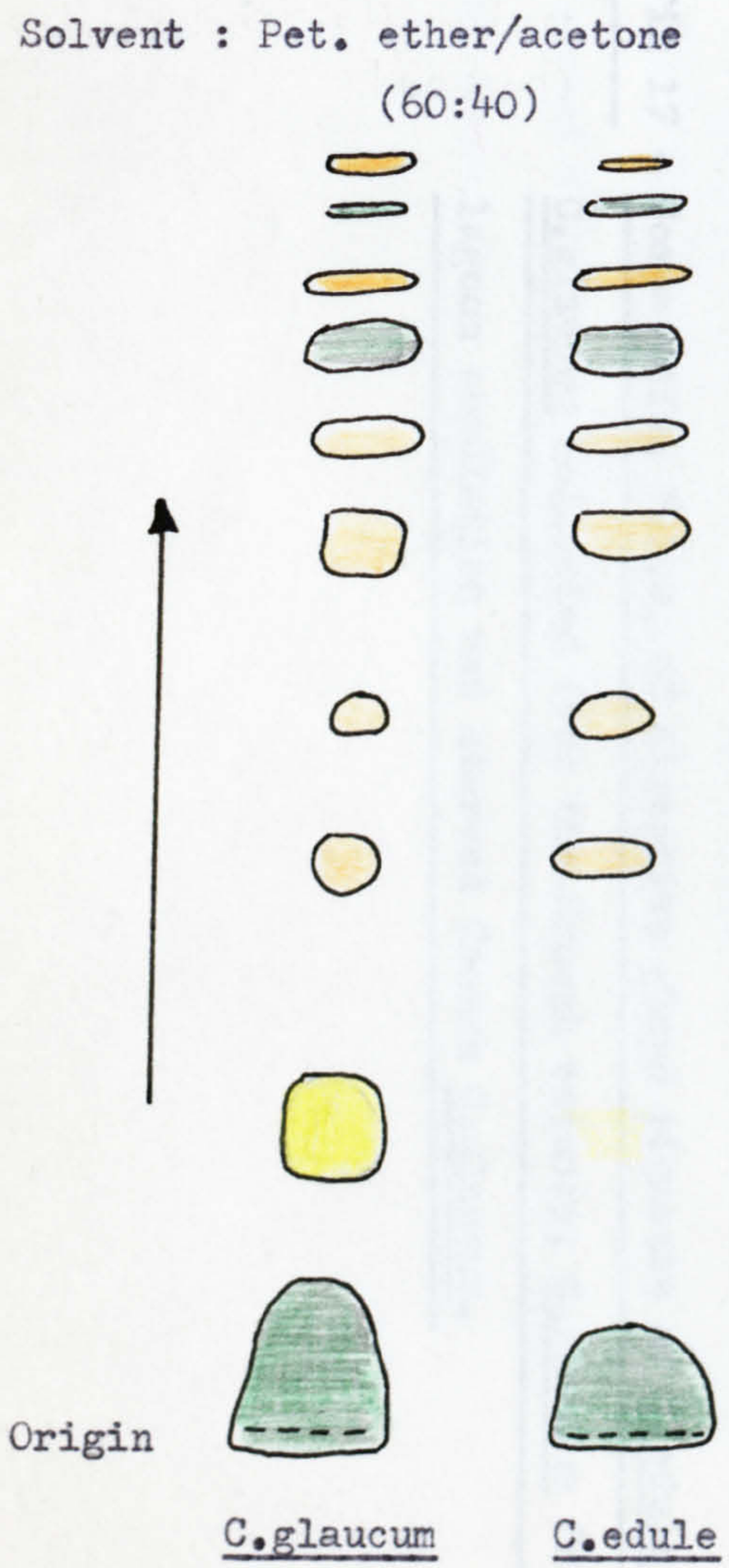


Fig 14 - Distribution of pigments from the digestive glands of cockles whose glands where similar in colour and morphology.

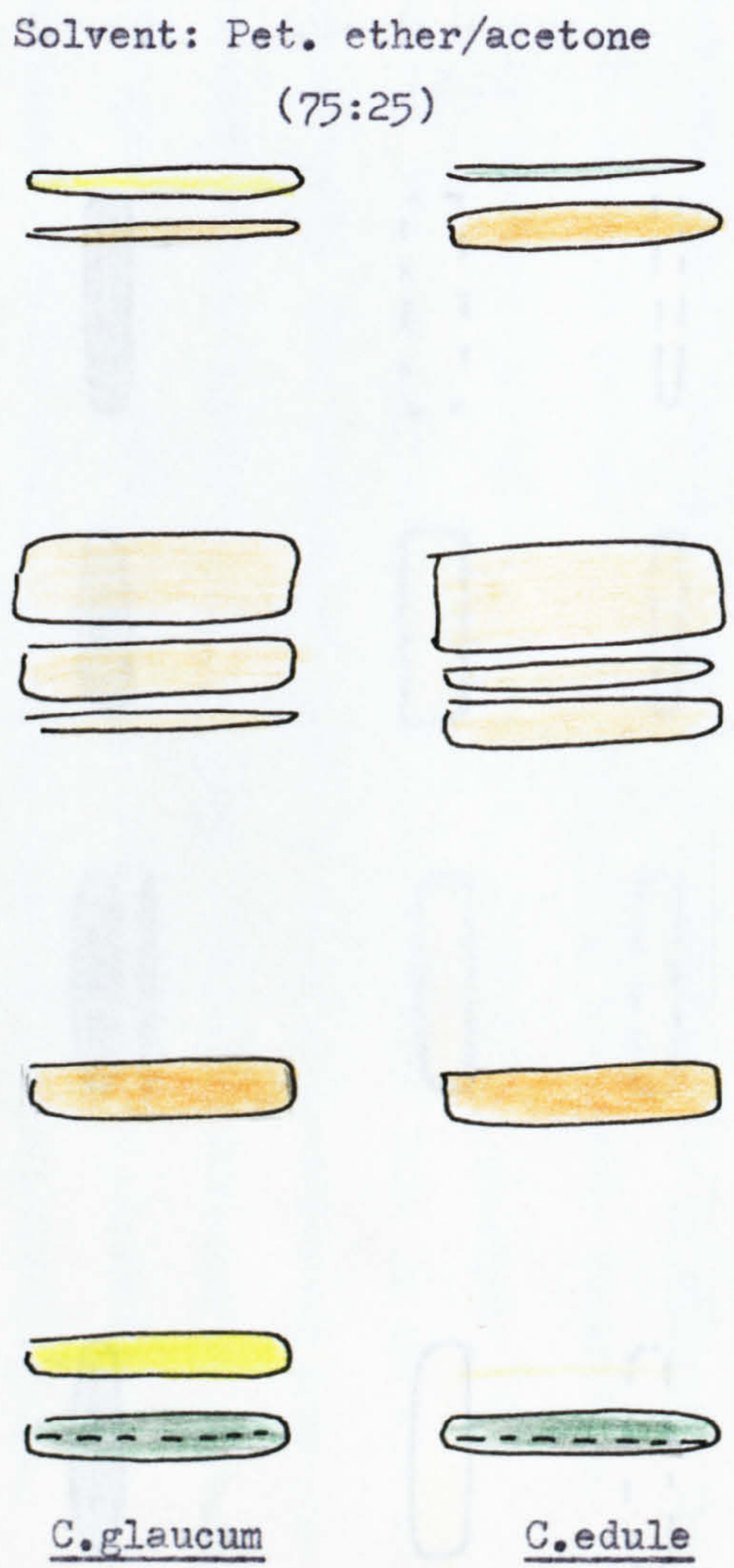


Fig 15 - Distribution of pigments from cockles starved for 2 weeks,
collected - 7. 4.69
examined -20. 4.69

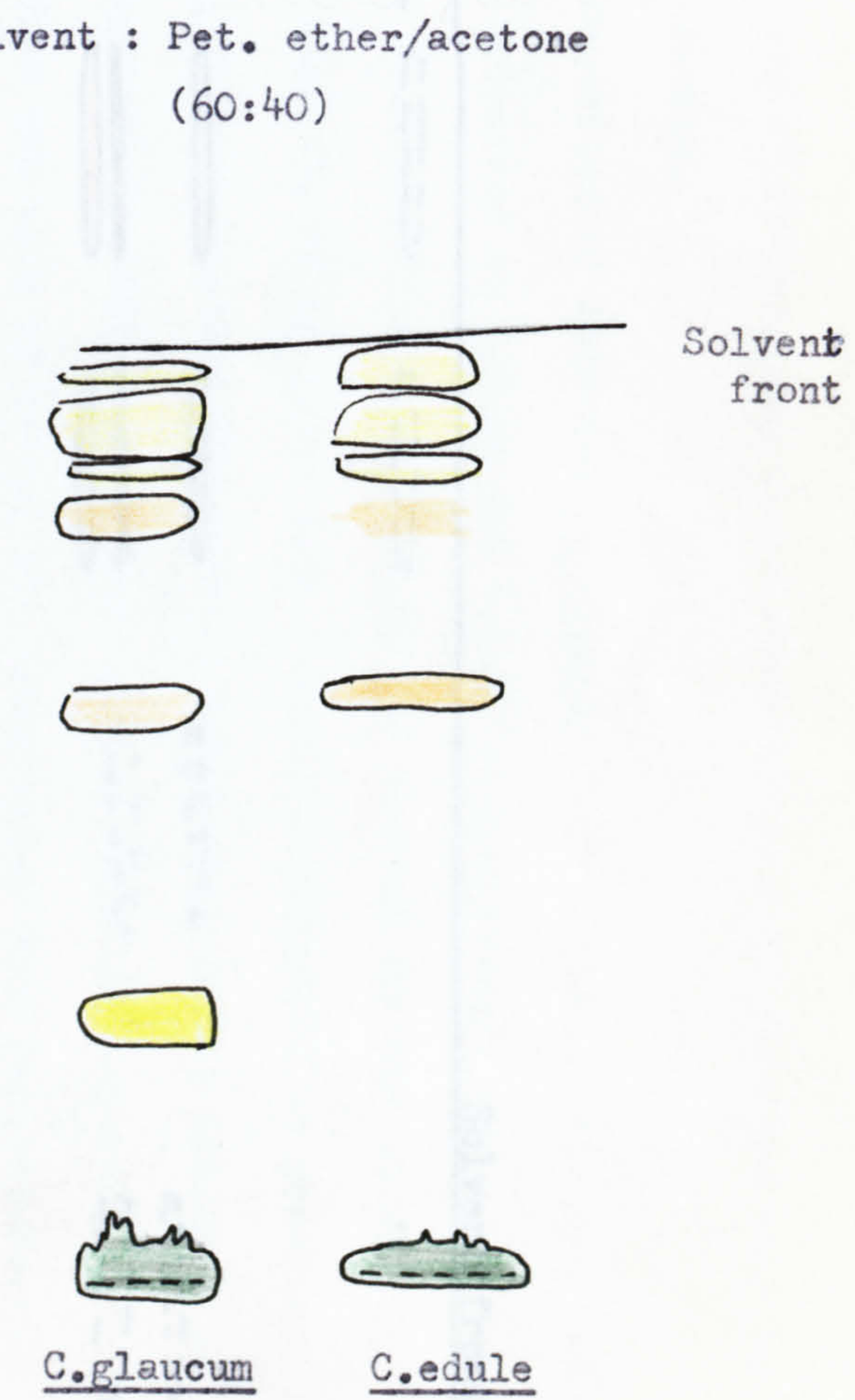
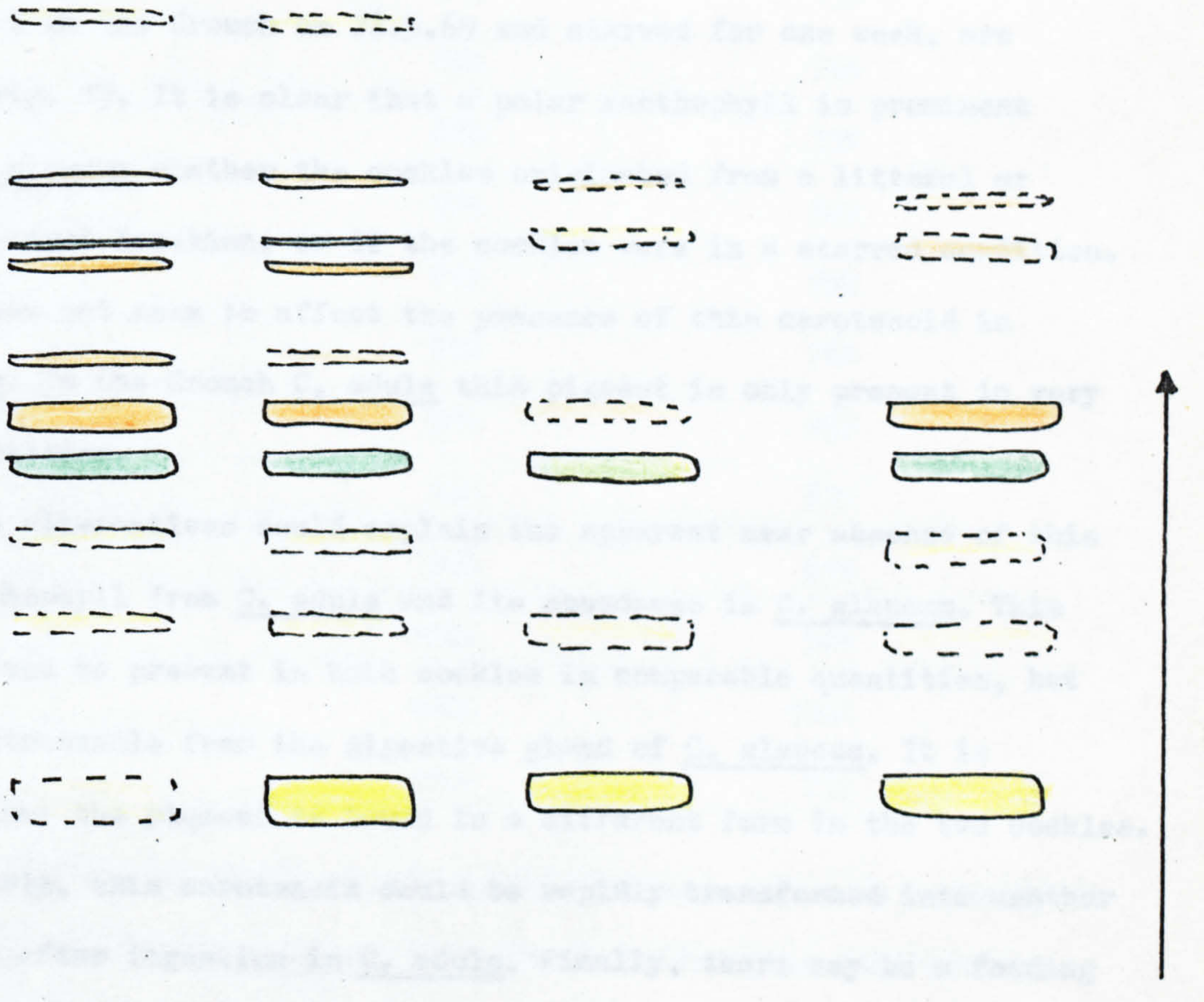


Fig 16 - Distribution of pigments of cockles starved for 25 days;
collected - 7. 4.69
examined - 2. 5.69



Collected on 4. 6.69 from the Crouch mixed cockle population.

Collected 6.6.69 from Gosport lagoon.

Originating from the Crouch population and starved for 1 week.

Fig 17 - Comparative T.L.C. of digestive gland pigments of C.edule and C.glaucum collected from the Crouch estuary; C.glaucum from a lagoon population and starved Crouch C.glaucum.

pigments are of interest as their chemical form is retained even in starved animals.

A comparison of lagoonal C. glaucum from Gosport, with the Crouch cockles (collected on 6.6.69 and 4.6.69 respectively), and C. glaucum collected from the Crouch on 28.5.69 and starved for one week, are shown on fig. 17. It is clear that a polar xanthophyll is prominent in all C. glaucum whether the cockles originated from a littoral or from a lagoonal location, or if the cockles were in a starved condition. Habitat does not seem to affect the presence of this carotenoid in C. glaucum. In the Crouch C. edule this pigment is only present in very small quantities.

Three alternatives could explain the apparent near absence of this polar xanthophyll from C. edule and its abundance in C. glaucum. This pigment could be present in both cockles in comparable quantities, but is only extractable from the digestive gland of C. glaucum. It is possible that the pigment is bound in a different form in the two cockles. Alternatively, this carotenoid could be rapidly transformed into another carotenoid after ingestion in C. edule. Finally, there may be a feeding difference between the two cockles. Certainly it is generally accepted that animals derive carotenoids from their food, originally plants (Goodwin, 1952), and thus it may well be that C. glaucum selects algae, flagellates and diatoms as food, more so than does C. edule. It was noted during the reproductive survey of the two Crouch cockles, that in winter the intestine of C. edule was packed with silt (detritus and bacteria), whilst the gut of C. glaucum often appeared to be devoid of silt. The incidence of silt packed in the intestine of the two cockles collected from the mixed population between 22.1.69 and 10.9.69 is shown overleaf:

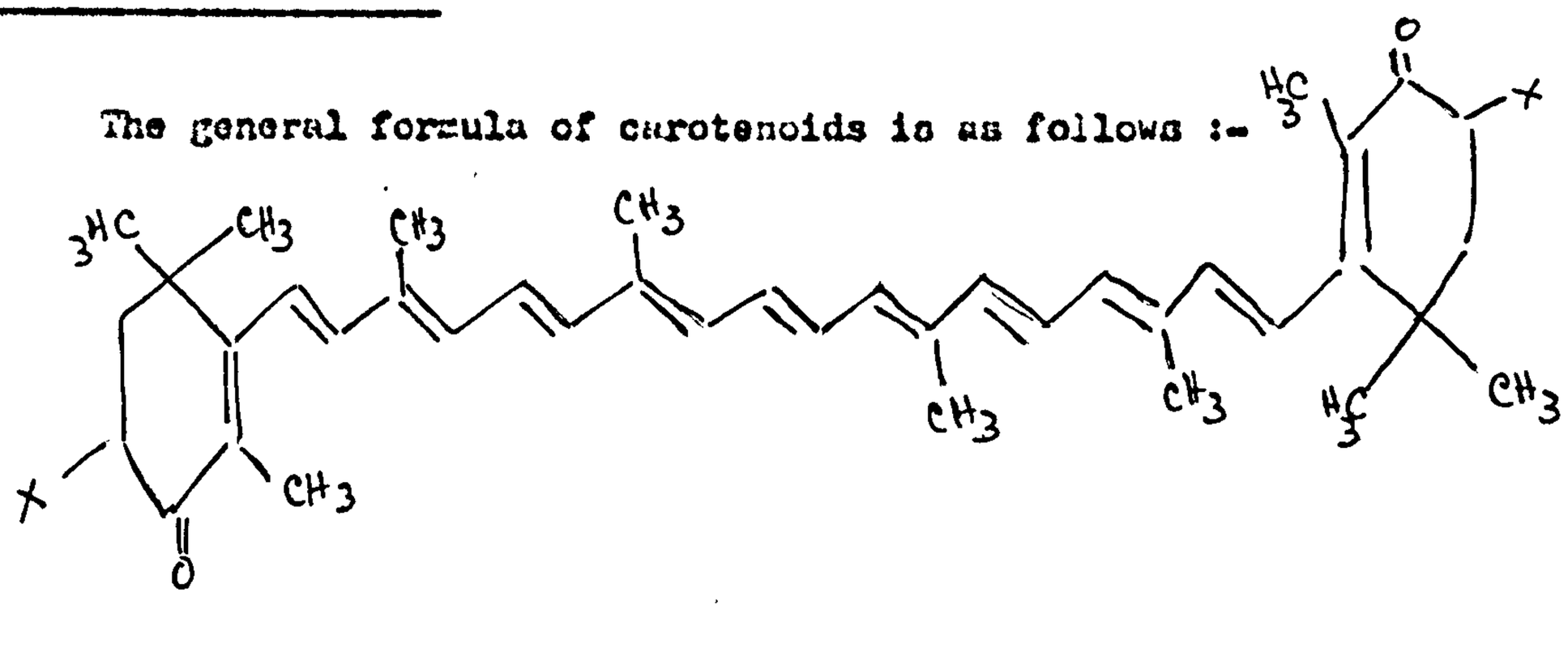
Percentage incidence of silt in the intestine of C. edule and C. glaucum from the Crouch mixed cockle population :

Date of sample	C. edule	C. glaucum
12.1.69	94%	13%
8.3.69	89%	35%
22.4.69	88%	15%
4.5.69	97%	30%
18.5.69	81%	95%
29.5.69	90%	76%
5.6.69	92%	95%
15.6.69	92%	87%
14.7.69	90%	61%
27.7.69	100%	50%
19.8.69	100%	100%
10.9.69	100%	73%

Clearly, the presence of silt in the gut occurred more commonly in C. edule than in C. glaucum, in individuals from the same environment. It might be expected that lagoonal C. glaucum would predominantly feed upon phytoplankton, as silt would seldom be maintained in suspension in the clear waters of such habitats. It could, therefore, be tentatively suggested that C. glaucum is predominantly an algal planktonic feeder, whilst C. edule is less selective, ingesting algae if they are available but also feeding upon the bacteria and detritus found associated with silt and fine muds.

5. Chemical investigation into the nature of the polar xanthophyll of Corastoderma glaucum.

The general formula of carotenoids is as follows :-



Thus, typically, carotenoids have a long hydrocarbon chain (chromatophore), with two terminal ionone rings. This general formula can be modified by the variable substitution of X and the substitution of other terminal groups.

Carotenoids in animals are originally derived from plants. Thus, although animals can modify a carotenoid molecule, chiefly by oxidation, they cannot synthesise a carotenoid from non-carotenoid precursors, (Green, 1963). It was hoped that, by identification of the carotenoid in the digestive gland of C. glaucum and by comparison with other known carotenoids from various algae, assumptions could be drawn as to the food preferences of this cockle. However, the number of known polar xanthophylls from algae or animals is not sufficiently comprehensive to allow such deductions to be made.

The chemical characteristics of the polar xanthophyll from C. glaucum are listed below :

* (1) Mass spectrophotometry indicated a molecular ion at m/e 600 (corresponding to a molecular formula of $C_{40}H_{56}O_4$). The cracking pattern of this xanthophyll is stated by Galesko (1970) to be similar to that extracted from Mytilus edulis (referred to by her as mussel band-1a).

(2) The xanthophyll gave an apparent hypochromic shift of 22.3 nm., indicative of a carotenoid epoxide group, upon treatment with acidified chloroform. One drop of this solution (10ml. $CHCl_3$ + 3 drops of concentrated HCl) was added to the xanthophyll dissolved in chloroform within a spectrophotometer cuvette (for result, see fig. 18). However, as the absorption spectrum for the acidified solution gave a very flat peak, the presence of an epoxide is not definitely proved.

(3) The absorption maxima recorded in a variety of solvents are shown below :

Solvent	maximum of absorption peaks of the polar xanthophyll from C. glaucum.		
Benzene	487	457	S (428)
Chloroform	484	455	S (428)
Carbon disulphide	508	477	S (451)
Ethanol	475	445	flat peak (400-415)
Acetone	476	447	S (424)

(4) The absorption spectra of known standards α and β -carotene, which have 2 and 1 conjugated double bonds in the inone rings respectively, have been compared with the cockle xanthophyll. From fig. 19, it can be seen that the main absorption maximum peak shifts to the left as follows :

---

* For the chemical evaluation of this polar xanthophyll, I am indebted to Miss J. Galesko of Professor Weeden's Carotenoid Research Group at Queen Mary College.

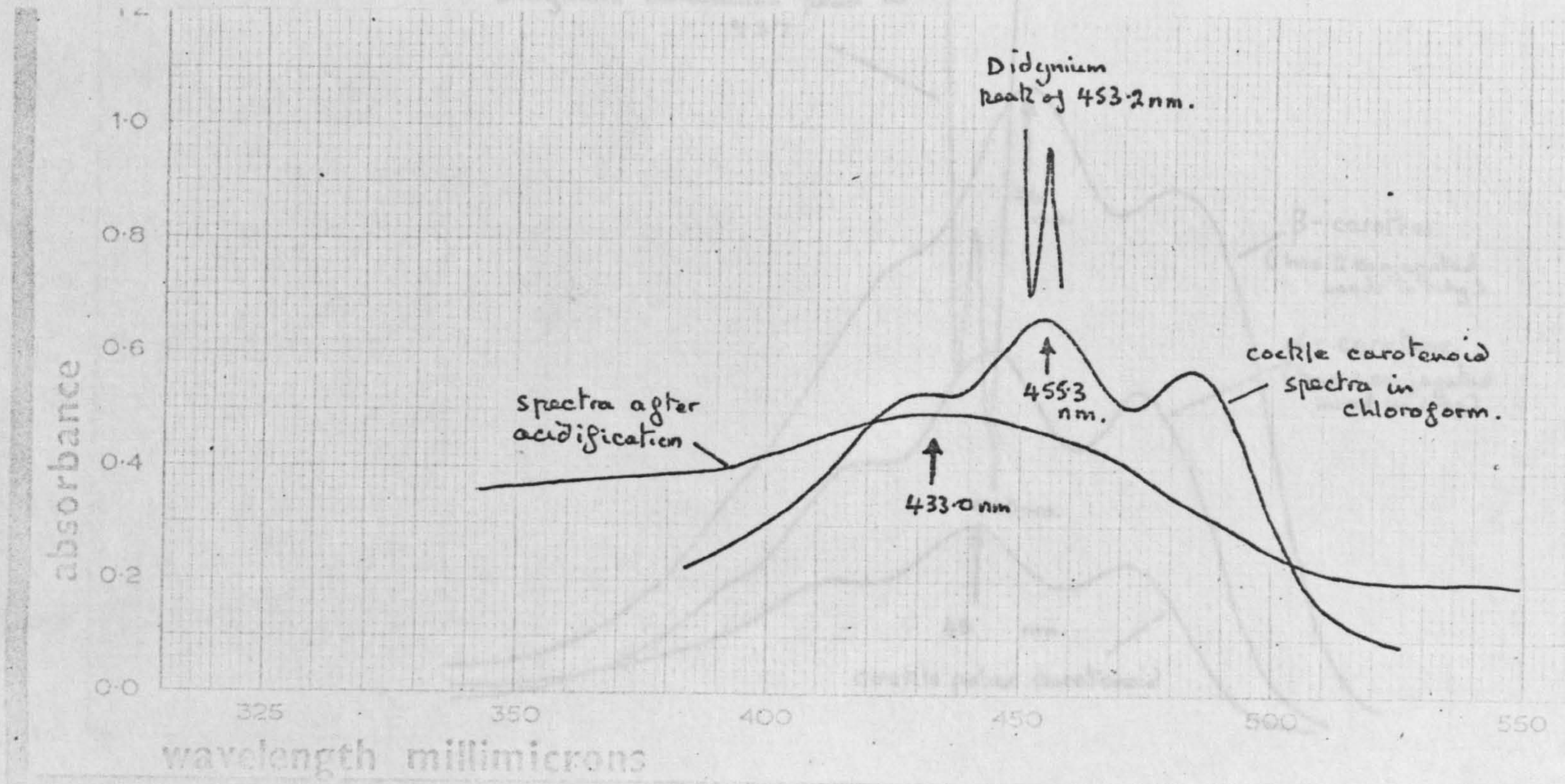


Fig 18 - Evidence of hypochromic shift in the chloroform spectrum of the cockle polar carotenoid upon acidification.

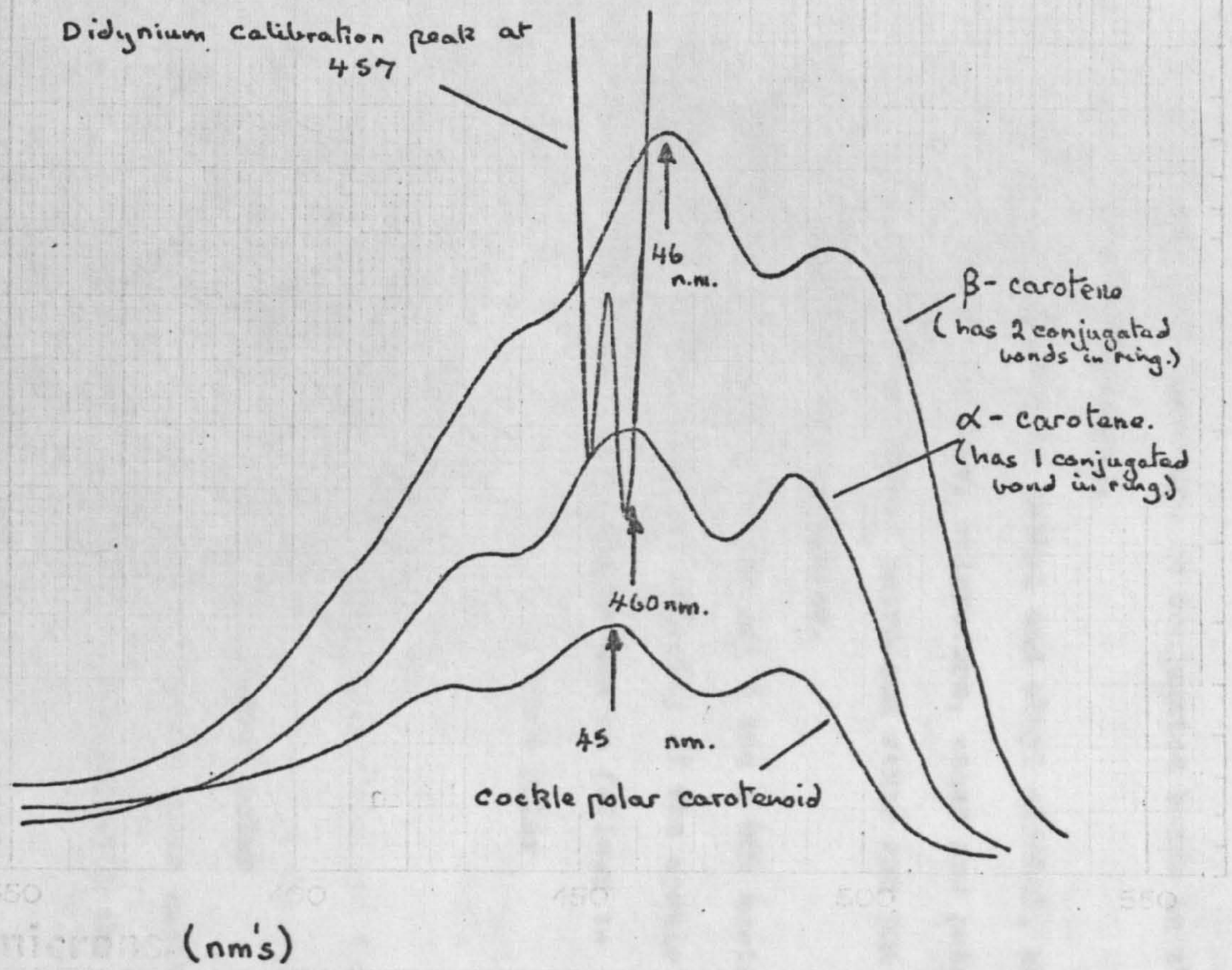


Fig 19 - Comparison spectra in benzene of α and β-carotene and the cockle pigment, to show shift of absorption peak to the left, indicating the absence of conjugated double bonds in the inone rings of the cockle carotenoid.

Main maximum from absorption spectra in benzene :

- carotene	- carotene	Cockle pigment
466.5 nm.	460 nm.	457 nm.
(2 conjugated bonds)	(1 conjugated bond)	

This suggests that there are no conjugated bonds in the inone rings of the cockle xanthophyll.

(5) The pigment was soluble in methyl and ethyl alcohol, acetone and water, but insoluble in benzene, chloroform, ether and petroleum ether (40/60°C). Using partition between petroleum ether and 90% methanol, this pigment dissolved in the hypophase.

(6) comparative T.L.C. using silica gel G and a 40% acetone in petroleum spirit solvent, showed that the polarity of the cockle xanthophyll compared with several other carotenoids was as follows :-

most polar

cockle xanthophyll

all trans neoxanthin

9 - cis neoxanthin

least polar

(Jałeśko (1970) is of the opinion that the polar xanthophyll extracted by her from Mytilus edulis is identical with the cockle xanthophyll.)

(7) On the T.L.C. plate, the bright yellow cockle xanthophyll faded slowly upon exposure to air and did not turn green or blue-grey, as do many other common carotenoids.

In a recent review, Weeden (1969) records the structure of known carotenoids. From this work, the molecular structure of the following

polar carotenoids have been extracted :

Carotenoid	Structure	Other comments
1. Violaxanthin	4 oxygen atoms, 2 epoxides	Galesko (1970) showed by comparative T.L.C. that the cockle xanthophyll was more polar than violaxanthin.
2. Neoxanthin	4 " " 1 "	Shown in comparative T.L.C. that cockle xanthophyll was more polar than neoxanthin.
3. Crustaxanthin	4 " " no epoxide	(as 1 above).
4. Astaxanthin	4 " " " "	
5. Astracene	4 " " " "	
6. Iso-fucoxanthin	5 " " " "	
7. Fucoxanthin	5 " " 1 "	
8. Diadinoxanthin	3 " " " "	
9. Siphonoxanthin	3 " " no "	(Structure from Kleinig, 1969).

Thus, neoxanthin, siphoxanthin, diadinoxanthin and fucoxanthin are nearest to the cockle xanthophyll. The recorded absorption λ max. for these xanthophylls are recorded below :

All figures, unless otherwise stated, are from Goodwin (1965).

Solvent	Neoxanthin			Siphoxanthin	
Benzene	477	447		-	
Chloroform	477	447	421	466[4]	
Carbon disulphide	494	462	437[3]	-	
Ethanol	467	438	417	445	451[4]
Acetone		-		-	
Petroleum spirit	466	437	415	478	450 (427)[4]

Solvent	Diadinoxanthin			Fucoxanthin		
Benzene	-			-		
Chloroform	-			492	457	
Carbon disulphide	506 (1) 506 (2)	475 474	450-2 (1) 442 (2)	510	477	445
Ethanol	478 (1) 476 (2)	447-8	426-8 (1) 425 (2)	(470)	466 (2)	
Acetone	-			-		
Petroleum spirit	-			478	450	425

(1) Extracted from Gilchrist & Green (1960)
(2) " " Allen (1960)
(3) " " Strain (1938)
(4) " " Ricketts (1967)

By comparison with the absorption spectral recordings obtained for the cockle xanthophyll, it appears that the carotenoid diadinoxanthin is the best approximate from this selection. However, in the recent literature, Strain et al. (1970) have the structural formula of heteroxanthin, a xanthophyll from species of the xanthophyceae, as molecular mass 600 and empirical formula $C_{40}H_{50}O_4$. This pigment is regarded by Strain et al. (1963) to be a neoxanthin like xanthophyll but chromophorically like diadinoxanthin. The absorption maxima of this xanthophyll in ethanol, 478, 448, 3(422-424) (Strain et al., 1970), is also very close to the values obtained for the cockle carotenoid. Heteroxanthin does not have an epoxide, as no isomerism of an epoxy-group to a furanoid group occurs upon acidification (Strain et al., 1970), but it must be noted that the presence of an epoxide in the cockle pigment has not been categorically proved.

Therefore, it would seem that the cockle polar xanthophyll may be close to either diadinoxanthin which has been isolated from various

chrysophyceae flagellates, (Green & Gilchrist, 1960; Dales, 1960), or heteroxanthin found in species of the xanthophyceae (Strain et al., 1968, 1970). In either case, it indicates that C. glaucum is concentrating the pigment within the digestive gland, but whether this is because the pigment accumulates in the digestive gland or because the cockle is selecting flagellates as food is uncertain.

6. Additional biochemical investigation into the magnesium content of the shells of C. edule and C. glaucum.

It has been suggested that the temperature and salinity of the environment affects the magnesium content of calcite and aragonite shells (Lowenstam, 1963). Lerman (1964) records an irregular increase in magnesium content of the calcite layers of the oyster, Crassostrea, with increase in temperature and he regards this increase as independent of the Mg^{++}/Ca^{++} ratio in the sea-water. He is of the opinion that variation in magnesium concentration could reflect genetic differences between semi-isolated populations of the oyster. Further, it has been demonstrated by Dodd (1965) that in Mytilus edulis, the magnesium content of the calcite prismatic and aragonite nacreous shell layers, differs within a single individual. Moreover, Price and Mallum, 1967, have shown that, in the cephalopod, Nautilus, the strontium content of secreted shell material varies appreciably and they conclude by suggesting that there is some biochemical control of secretion within the individual.

Thus it appeared possible that, if the biochemistry of the two cockles differed, the minor constituents of the shell of these cockles could also differ. As magnesium is the central atom of the chlorophyll nucleus and as a difference in breakdown of chlorophyll in the two cockles

was suspected (see earlier), it was considered possible that the magnesium content of the shells of C. edule and C. glaucum might not be identical. This argument would require that the magnesium incorporated in the shell was derived from the tissue fluids and not from the external sea-water. The fact that shells from high temperature environments also have high magnesium contents, (Lowenstam, 1963), may reflect the increased metabolism of individuals from these environments. Thus, if magnesium is extracted from the sea and incorporated in the shell purely accidentally, it would be reasonable to suppose, assuming that the magnesium ion content of the water is constant at different temperatures, that the magnesium in the shell would also be constant per unit shell deposited. The observed increase in magnesium content could be explained by an increase in feeding rate over growth rate to cover the higher metabolism at higher temperatures. More chlorophyll would consequently be broken down by the digestive enzymes, thus releasing more magnesium into the body fluids. This could then account for the greater quantities of magnesium in the shells from higher temperature environments. Incorporation of magnesium from the tissue fluid could explain the fluctuations of magnesium content of shells from different temperature regimes.

Methods.

Cockles of the two types, C. edule and C. glaucum, were collected from the mixed cockle population of the Crouch, Essex. The body tissues were removed and the shells thoroughly cleaned in a 5% solution of sodium hypochlorite to remove any organic matter and finally washed in distilled water.

The magnesium content of the shells was analysed using a Unicam

S.P. 90 Atomic Absorption spectrophotometer. A magnesium lamp was used at a wavelength of 2861 Å and slit width of 0.09 cm.* Standards of magnesium oxide were made up by dissolving 8 mg. MgO + 50 mg. $CaCO_3$ in 10 mls. of 10% hydrochloric acid and diluting with distilled water. From these solutions, a calibration curve for MgO content was obtained.

The left valve from each valve pair was ground to a fine powder and thoroughly mixed. A small sample of this powder (about 50 mg.) was removed and accurately weighed to 5 decimal places. The shell was then dissolved, diluted to 100 mls. and treated as were the standards. From the calibration curve, the quantity of shell MgO could be determined and the percentage in the total shell calculated. The results for the two cockles from a common environment are shown below :

Percentage MgO content of the left valve of the two Cerastoderma from the Crouch mixed cockle population.

Cerastoderma edule (n = 14)		Cerastoderma glaucum (n = 14)	
0.043	0.051	0.049	0.038
0.049	0.041	0.045	0.043
0.041	0.041	0.044	0.047
0.039	0.040	0.037	0.049
0.037	0.044	0.037	0.041
0.049	0.044	0.040	0.043
0.047	0.048	0.068	0.041
Total - Σx_1 = 0.614		Total - Σx_2 = 0.622	
Mean percentage x_1 = 0.0483		x_2 = 0.0444	

These mean values are not significantly different.

Clearly, the average percentage content of MgO in the shells does not vary between the two cockles.

---

* I should like to acknowledge the technical assistance of Mr. S. Adams of the Geological Department, Queen Mary College, in the experimental work recorded in this section.

amples of shell of about 20 - 40 mg. in weight were removed from the innermost and outermost shell layers. These were analysed separately and finally the whole shell was ground up, as before, and the average magnesium oxide content determined. The variation in percentage MgO content in these shell samples is shown below :

	Percentage MgO content		
Cockle type	Whole value	Inner layer	Outer layer
C. edule	0.060	0.049	0.118
C. edule	0.047	0.034	0.071
C. edule	0.048	0.024	0.096
Mean values	0.052	0.036	0.095
C. glaucum	0.041	0.021	0.081
C. glaucum	0.043	0.016	0.063
C. glaucum	0.041	0.015	0.068
Mean values	0.042	0.017	0.071

In all cases, the inner nacreous layer contained much less magnesium than the outer prismatic layers. This factor ranged from about 1:3 in C.edule to about 1:4 in C. glaucum.

Mallan & Price (1967) using X-ray diffractometry, state that the two shell layers of the Carastoderma shell consist only of aragonite. The form of the calcium has been determined here by infra-red spectrophotometry.

Using an 'in-disc' technique, an approximately 1 mg. sample of shell was ground to less than 2 μ particle diameter and then ground

intimately with 150 mg. KCl (spect. pure). The disc was formed by pressure (10 tons) under vacuum for 2 minutes and then mechanically extruded. The infra-red scan of samples from the inner and outer shells are shown on figs. 20 and 21. Clearly some calcite is present in the basically aragonitic matrix of the Cerastoderma shell. By comparing with standard aragonite/calcite mixtures, it would appear that a little less than 8% calcite was detected in the inner layers, whilst only 1 - 2% occurs in the outer layers. It is possible that some of the metastable aragonite of the shell has been converted, in the preparation of the disc, to the more stable calcite, but as this technique has previously been used successfully with no such conversion, this would appear to be unlikely.

In general, where the calcite content of the shell increases, the magnesium content is also greater (Chave, 1954). The above pattern in the Cerastoderma shells does not fit this trend as the inner layers, which appear to contain more calcite, have lower magnesium contents than the outer shell layers. There are, however, other examples in the literature where the magnesium content of the calcite region is lower than the aragonitic shell region (see Wilbur, 1964). The presence of a small percentage of calcite in the main aragonitic matrix was noted in both C. edule and C. glaucum.

In summary, no major differences in average magnesium content of the shell were found between C. edule and C. glaucum from a common environment.

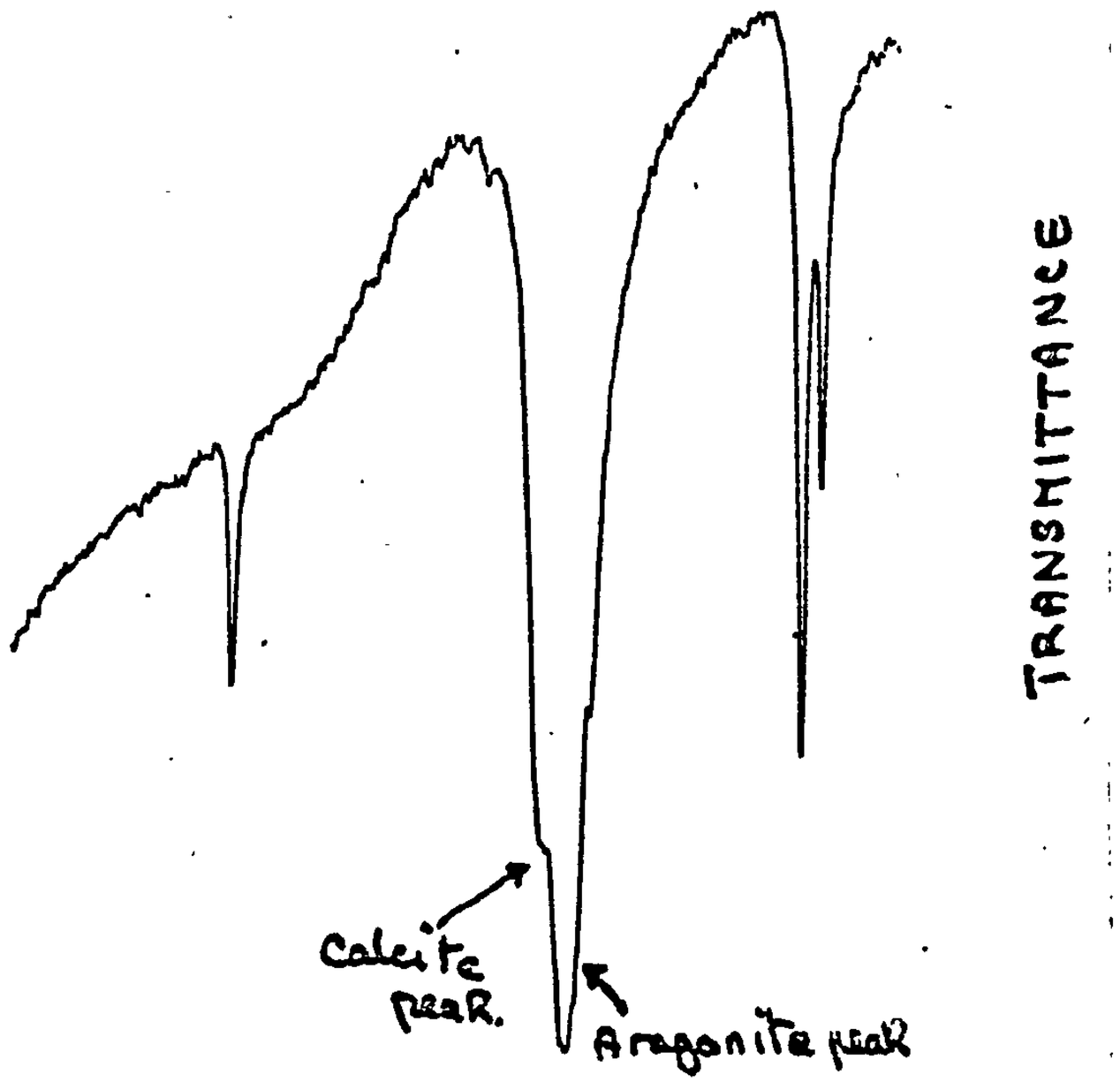


Fig 20 - Infra - red spectrum of the outer (or prismatic) shell layers.

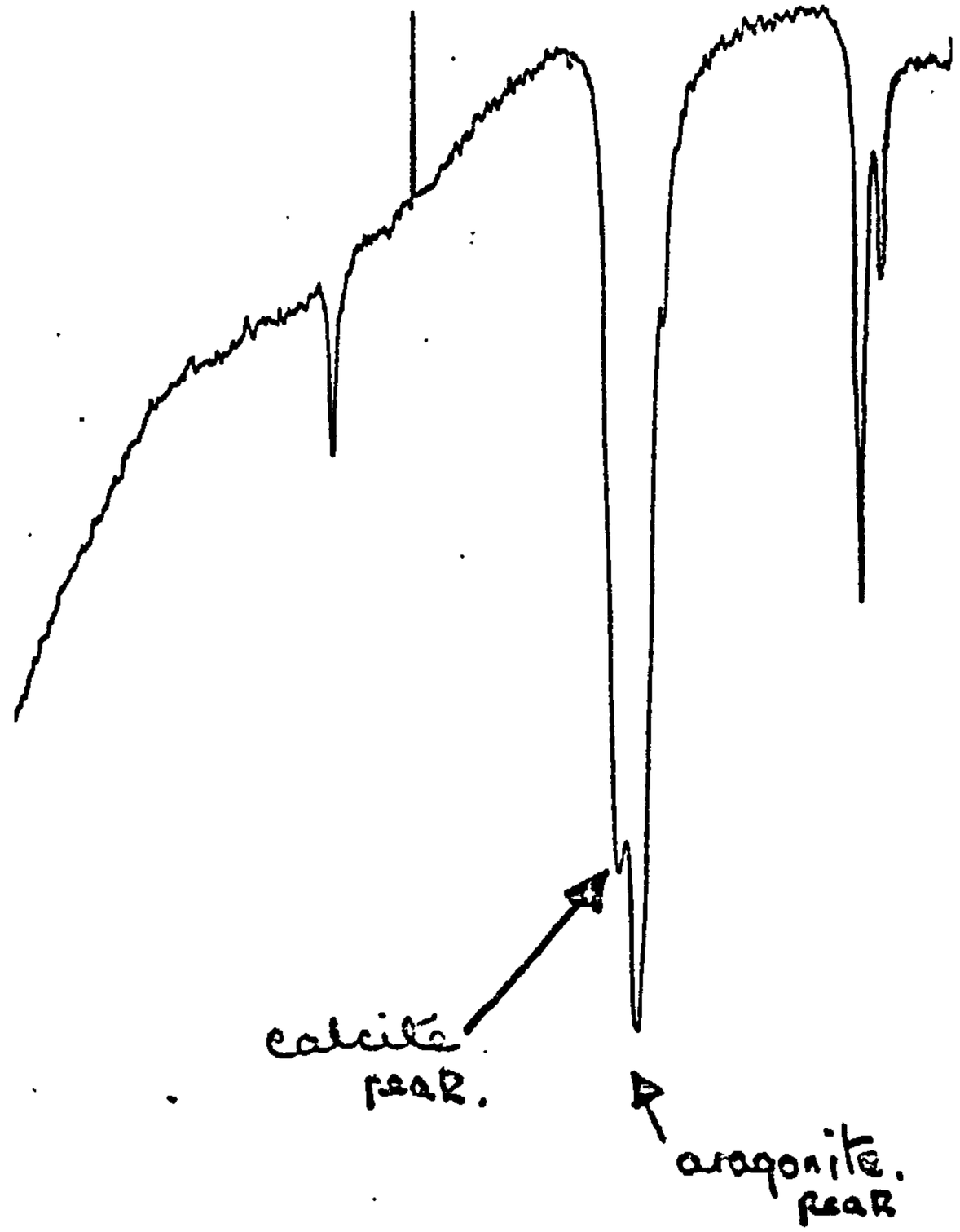


Fig 21 - Infra - red spectra of the inner (or nacreous) shell layers.

REFERENCES

BARNES, H.,
/BARNES, H., & FINLAYSON, D.M., 1963. The seasonal changes in body composition and oxygen uptake of two common boreo-artic cirripodes Balanus balanoides and B. balanus. J. mar. Biol. Ass. U.K., Vol. 43, pp. 185-211.

BARRETT, J., 1968. Lipids of the infective and parasitic stages of some nematodes. Nature Vol. 218, pp. 1,267-1,268.

BLANK, M.L., et al, 1964. Quantitative analysis of Lipids by Thin-Layer Chromotography. J. Am. oil. Chems. Soc. Vol. 41(5) pp. 371-376.

BOYDEN, C.R., 1969. Ecology of the cockle Cardium glaucum Bruguière. Essex Nat. Vol. 32, (3), pp. 223-226.

BROWN, J.S., 1963. Forms of Chlorophyll-a Photochem and Photobiol. (Chlor. Metabol. Sym.), Vol. 2, pp. 159-173.

BUZZATI-TRAVERSO, A.A. & RECHNITZER, A.B., 1953. Paper Partition Chromatography in Taxonomic studies. Science, Vol. 117, no. 3029, pp. 53-59.

CAMPBELL, B.A., 1968. Studies on cartoenoids in Mytilus and its parasites. Ph.D. Thesis, London.

CHAVE, K.E., 1954. Aspects of the biogeochemistry of magnesium (i) Calcareous marine organisms. J. Geol. Vol. 62, pp. 266-283.

CONNELL, J.J., 1953 . (a) I- Electrophoretic analysis of codling extracts of low ionic strength. Biochem. J. Vol. 54, pp. 119-126.

CONNELL, J.J., 1953. (b) II- Electrophoretic analysis of the low ionic strength extracts of several species of fish. Biochem. J. Vol. 55, pp. 378-388.

DALES, R.P., 1960. On the pigments of the Chrysophyceae J. mar. biol. Ass. U.K. Vol. 39, pp. 693-699.

DODD, J.R., 1965. Environmental control of strontium and magnesium in Mytilus. Geochim. Cosmochim. Acta., Vol. 29, pp. 385-398.

FOX, A.S., 1965. Application of paper chromatography to Taxonomic studies. Science, Vol. 126, p. 143.

GALESKO, G., 1970. Structural studies on carotenoids. Ph.D. Thesis, London.

GEISE, A.C., 1967. Some methods for study of the biochemical constitution of marine invertebrates. Oceanogr. Mar. Biol. Ann. Rev. Vol. 5, pp. 159-186.

GEISE, A.C., 1969. A new approach to the biochemical composition of the mollusc body. Oceanog. mar. Biol. Ann. Rev. Vol. 5, pp. 159-186.

GEISE, A.C. & HART, M.A., 1967. Seasonal changes in component indices and chemical composition in Katherina tunicata. J. exp. mar. Biol. Ecol. Vol. 1, pp. 34-46.

GEISE, A.C., HART, M.A., SMITH, A.M. & CHEUNG, M.A., 1967. Seasonal changes in body component indices and chemical composition in the Pismo Clam, Tivela stultorum. Comp. Biochem. Physiol. Vol. 22, pp. 549-561.

GEORGE, J.C. & PATEL, B.S., 1956. The seasonal variation in the fat content of the liver and gonads in a marine and fresh water decapod. J. anim. morph. and physiol. Vol. III(1), pp. 49-55.

GILCHRIST, G.M. & GREEN, J., 1960. The pigments of Artemia. Proc. Roy. Soc. (B), Vol. 152, pp. 118-136.

GOEDHEER, J.C., 1967. Les changements du spectre d'absorption et de fluorescence au cours du verdissement et du vieillissement des plastes. Le Chloroplaste, Croissance et vieillissement. Ed. C. Sironvul et cie Editeurs Published Maison.

GOODWIN, T.W., 1952. The comparative Biochemistry of the carotenoids. Chapman & Hall, London.

GOODWIN, T.W., 1965. Chemistry and Biochemistry of Plant Pigments. Academic Press, London and New York.

GREEN, J., 1963. Seasonal polymorphism in Scapholeberis mucronata (O.F. Müller)(Crustacea: Cladocera). J. anim. Ecol. Vol. 32, pp. 436-425.

KLEINIG, H., NITSCHE, H., & EIGER, K., 1969. The structure of siphonaxanthin (Algal carotenoid) Tetrehedron letters No. 59, pp. 5139-5142.

LEONE, C.A., 1964. Ed. Taxonomic biochemistry and serology. New York, Ronald Press.

LERMAN, A., 1964. Strontium and Magnesium in water and in Crassostrea calcite. Science, Vol. 150, pp. 745-751.

LOWENSTAM, H.A., 1963. Biologic problems relating to the composition and diagenesis of sediments. In the Earth Sciences - Problems and Progress in Current Research, edit. T.W. Donnelly, pp. 137-195, Univ. of Chicago Press.

MANGOLD, H.K., 1961. Thin-layer Chromatography. J. Amer. oil chem. Soc. Vol. 38, pp. 708-727.

MANGOLD, H.K., 1965. Aliphatic Lipids in Thin-Layer Chromatography. Ed. E. Stahl. Academic Press, New York and London.

MANWELL, C., 1966. Sea-cucumber sibling species: polypeptide chain types and oxygen equilibration of hemoglobin. Science, N.Y., Vol. 152, pp. 1393-1396.

MANWELL, C. & KERST, K.V., 1966. Possibilities of biochemical taxonomy of bats using hemoglobin, lactate dehydrogenases, esterases and other proteins. Comp. Biochem. Physiol. Vol. 17, pp. 741-754.

MANNELL, et al., 1967. Biochemical differences between Calanus finmarchicus and C. helgolandicus. J. mar. biol. Ass. U.K., Vol. 47, pp. 145-169.

MORTON, B., 1970. The tidal rhythm and rhythm of feeding and digestion in Cardium edule. J. mar. biol. Ass. U.K., Vol. 50(2), pp. 499-512.

PADLEY, F.B., 1964. Thin-layer Chromatography of Lipids in 'Thin-layer Chromatography. Ed. Marini-Bettolo G.B. Sci. Reports of the Institute Superoino di Sanita Elsevier Pub. company pp. 87-115.

REED, K.K., 1964. Chromatographic Comparisons of the parotid gland secretions of six species in the Bufo vallicens group. In 'Taxonomic Biochemistry and Serology'. Ed. C.A. Leone, pp. 451-464.

PRICE, N.B. & HALLAM, A., 1967. Variation of strontium content within shells of recent Nautilus and Sepia. Nature Vol. 215, pp. 1272-1274.

RANDERATH, K., 1963. Thin-layer Chromatography. Academic Press. New York and London, pp. 126-151.

REID, R.G.B. & DUNNIL, R.H., 1969. Specific and individual differences in the esterases of members of the genus Macoma (Mollusca: bivalvia). Comp. Biochem. Physiol. Vol. 29, pp. 601-610.

RICKETTS, T.R., 1967. Further investigations into the pigment composition of green flagellates possessing scaly flagella. Phytochemistry, Vol. 6, pp. 1375-1386.

SIBLEY, C.G., 1960. The electrophoretic patterns of avian egg-white proteins as taxonomic characters. Ibis, Vol. 102, pp. 215-284.

SMITH, I. & STEVENS, H.G., 1969. Lipids. In 'Chromatographic and Electrophoretic techniques, Vol. I - Chromatography Ed. I. Smith (3rd Edition) pp. 437-449.

SMITH, J.H.C. & BENITEZ, A., 1955. Chlorophylls: Analysis in Plant materials in 'Modern Methods der Pflanzenanalyse' Eds. K. Paech and M.V. Tracey, Vol. 4, Springer, Berlin, pp. 142-196.

SPECTOR, W.S., 1963. Handbook of Biological Data. Saunders Company, Philadelphia and London.

STRAIN, H.H., 1938. 'Leaf Xanthophylls'. Carnegie Institute Publ. No. 490, Washington.

STRAIN et al, 1968. Molecular weights and empirical formulas of the Xanthophylls of Vaucheria. Phytochemistry, pp. 1417-1418.

STRAIN, et al., 1970. Structure of Heteroxanthin, a unique xanthophyll from the xanthophyceae (heterokontae). Chem. commun., Vol. 14, pp. 875-877.

WELSON, B.C.L., 1969. Spectroscopic methods for eluciating the structures of carotenoids. Vision, Springer-Verlag., New York.

WILBUR, K.A., 1964. Shell formation and regeneration in Physiology of Mollusca, Vol 1. Ed. Wilbur, K.M. and Yonge, C.M., pp. 243-282. Academic Press, New York and London.

WILSON, A.C. & KAPLAIN, N.O., 1964. Enzyme structure and its relation to taxonomy. In 'Taxonomic biochemistry and serology' pp. 321-346. Ed. C.A. Leone, New York, Ronald Press.

GENERAL CONCLUSIONS

From this comparative investigation of the differences between C.edule and C.glaucum some general conclusions have become apparent and they have been listed below:-

C.edule is predominantly a littoral animal inhabiting situations where some water movement occurs, whilst C.glaucum is found typically in stagnant, saline lagoons. Where this cockle occurs on the shore it is only found in sheltered locations.

The distribution of C.glaucum in Eire seems to be restricted to the western coasts. The lagoon populations of this cockle in south-east England are considered to be remnant populations.

Saline lagoons such as have been studied in this survey would appear to be far more stable environments than commonly supposed.

The lowest limits of salinity tolerance of C.glaucum supports the validity of the ecological delimitation of a zone within brackish waters in the region of 8-10‰ salinity.

The digestive gland of C.glaucum is always black, whilst the colorr and morphology of the gland is variable in C.edule.

C.edule air-breathes during aerial exposure at low tide. C.glaucum when it occurs on the shore does not exhibit any behaviour associated with air breathing.

It would appear that shell-ribbing is differently determined in the two cockles.

The hinge parasite Meiogymnophallus minutus which commonly infects C.edule is completely absent from C.glaucum. Another parasite Cercaria Bucephalopsis haimeana, often found in C.edule, occurs only very rarely in C.glaucum.

Considering the logarithmic data of ligument length to shell breadth it would seem that the variance is greater in cockles from a mixed population compared with separate cockle populations.

The presence of a very polar carotenoid in the acetone extracts of the digestive gland of C.glaucum in contrast to C.edule may be an indication of a feeding difference between the two cockles. It is suggested that C.glaucum is selecting unicellular algae as food, whilst C.edule would appear to be less selective, ingesting large quantities of silt.

Considering the Crouch mixed cockle population it has been shown that C.edule spawned seven weeks before C.glaucum in two successive seasons.

Evolutionary Considerations

Grosser (1955) quoting Mayr (1941, 1942 and 1949) defines the sequence in divergent allopatric speciation in the following manner: (1) Phenotypic variation adapted to environmental stresses, (2) Genetic fixation of adapted types by natural selections within reproducing populations or demes. (3) Isolation of selected populations by geographical barriers (or solely by large distances) sufficient to prevent gene interchange with other demes and (4) establishment of sufficient differences, so that reproductive isolation is effective even if later the original populations come together again. The process of sympatric speciation is regarded as more catastrophic, occuring as a result of chromosomal aberrations, e.g. polyploidy. The factor (3) in the above argument has been suggested by Lack (1949) to be open to another interpretation in the ecological isolation may be the result rather than the cause of speciation.

The two cockles could be considered to fall within the outlines of the above scheme. The two forms have become separated by habitat preferences; C.edule being littoral and C.glaucum being lagoonal. The Crouch mixed population can be regarded to be a convergent sympatric association of the two cockles, subsequent to the initial divergence. The analysis of the symbiont fauna tends to suggest that C.glaucum diverged from an edule type stock in the specialised habitat of saline lagoons. In the mixed population reproductive isolation between the two gene pools has been achieved. Thus the relationship between the two cockles is considered to be at a specific level, and C.edule and C.glaucum are regarded to be an example of a recently speciated, closely related species pair.

References

Quoted by Prosser (1955):

LACK, D., 1949. The significance of ecological isolation. pp. 299-309 in Jepsen, Mayr and Simpson. See below Mayr (1949).

MAYR, E., 1941. Speciation phenomena in birds. Biol.Symp. Vol.2. pp.59-88.

MAYR, E., 1942. Systematics and the origin of species. New York: Columbia Univ. Press.

MAYR, E., 1949. Speciation and systematics. Chap.14. pp.281-298 in Jephsen, Mayr and Simpson, 'Genetics paleontology and evolution'. Princetown Univ. Press.

PROSSER, C.L., 1955. Physiological variation in animals. Biol. Rev. Vol.30, pp. 229-262.

Appendix 1

British Museum (Natural History section) specimens.

Collections of the Museum Cerastoderma were examined on the 22.2.70. The morphological shell characters formulated by Høpner-Petersen (1958) to separate C.edule and C.lamarchi (= glaucum) have been applied to the Museum cockles. The specimens noted below are wrongly classified in the Museum collections as Cerastoderma edule (L.)

a. Tray No. 36/11. Cardiidae.

Cerastoderma (Cerastoderma edule)

Linnaeus 1758

1. Cerastoderma (C.) edule. Ex. Cooper Acc. No. 2 50 - 1 specimen. Collected from Southwold brackish water. Distorted specimen but could well be an example of a 'globose' C.glaucum.

2. Cockles collected from foreshore of Blackwater by D.C. Davis in May 1965. One thick-shelled individual of C.glaucum. Shell morphological evidence supported by complete absence of internal purple staining of posterior of shell. Remainder of sample normal thick-shelled C.edule.

3. Cerastoderma edule (Linnaeus) collected from Lake Fascia, E.S. of Oases of Giarabut, Libia, April 1957 - R. Brandt coll.

all. C.glaucum

4. Cerastoderma (C.) edule. Europe from H. Cuming coll.

Acc. No. 1829. 4 specimens.

Two largest shells definitely C.edule

Other two:- 1 definitely C.glaucum (internal staining diffuse brown around the valve periphery, shading into purple towards umbro is typical of C.glaucum not C.edule. All shell morphological characters point to C.glaucum.

- 1 irregularly shaped, cannot be categorised into either form.

5. Cockles from Portsea. Old collection ex Dr. J. Goodall.

5 specimens. All thin-shelled, typical of lagoon population of C. glaucum. (Shells described by Forbes & Hanley (1856) from the Hampshire Marshes.)

6. Cerastoderma C. edule.

1843. 6.8.37. from Aberdour. viii 1823.

12 specimens + 1 valve.

Heterogeneous selection of cockles.

2 largest C. edule, thick-shelled. Rest are smaller, have typical appearance of thin-shelled C. glaucum from a lagoon site.

B. Tray 36/10. Cardiidae Laevicardiinae.

Cerastoderma (barasiensis - edule).

1. Cockles from New England Creek by G.H. Spooner.

Brackish water, living in Chaetomorpha.

C. glaucum - typical lagoon type. Half of individuals without any internal shell staining.

2. Selection of specimens from the Eastern Mediterranean.

Must be regarded as forms of C. glaucum.

Shell morphology is more similar to the above than it is to C. edule.

3. C. edule from Hastings. 1847. 12.29.251. 1 specimen is C. glaucum.

4. C. edule from Reculver, Kent. Ex Cooper Acc. No. 2150.

2 specimens.

Both C. glaucum thick-shelled type.

5. C. edule. 1937. 2.9, 19-25. from Jury's Gut, borders of Kent and Sussex. Ex Tombin.

7 specimens. All thin-shelled C. glaucum.

C. Tray 36/12. Cardiidae, Laevicardiinae.

C. edule (vars.) - paludosa.

1. Cerastoderma edule var beltica. Reeve 1845.

Brackish water lagoon near Coalhouse Point, East Tilbury Marshes.

22.9.62.

Coll. J. Cooper in Chaetomorpha.

= C. glaucum.

2. C. edule var rustica. 2 specimens.

From Galway Bay, 1870, fairly large, fairly thick-shelled C. glaucum and one very thick shelled C. edule.

3. C. edule var rustica. Weiner coll. Acc. No. 1480.

from St. Nicholas Marshes,

are lagoonal C. glaucum, fair number without any internal staining.

Appendix 11

A. Legend for distribution of Cerastoderma edule (L.) around the British Isles.

1. = Localities where C. edule have been collected by the Author.

Information concerning the distribution of this cockle has been accumulated from various sources. The following biologists, whose assistance is gratefully acknowledged, are listed below:-

2. D.S. McLuskey, Univ. of Stirling, Scotland.

   - Ythan estuary, Torryburn, Scotland.

3. I.S. Mitchell (Miss). Univ. of Lancaster, Lancs.

   - Morecombe Bay, Lancs.

4. E.A. Bowers, Regent Street Poly. London, W.1.

   - Kyle of Tonge, Llanrhidian sands, Portsmouth.

5. W. Clifford-Jones, Univ. College of N. Wales, Bangor.

   - Wirral peninsula, Conway, N. Wales.

6. R. Seed, Queens College, Univ. of Belfast, N Ireland.

   - Padstow, Cornwall.

7. Clyde Marine fauna, ed. J.A. Allen.

   and H. Barnes, Marine Station, Millport Isle of Cumbrae, Scotland.

   - Clyde area, Cumbrae-Bute Isles, Fairlie sands, Millport.

8. J.A. Allen, Dove Marine laboratory, Cullercoats, Northumberland.

   - Northumberland coast, Holy Island, Budle Bay, Cowpen, (River Blyth estuary).

9. J. Drinkwater, Marine laboratory, Torry, Aberdeen.

   - St. Margarets Hope, Orkney, Dornock Firth, Kyle of Tongue, Leuchans, Traigh Mhor, Barra, Outer Hebrides, Carry Point Kyles of Bute, Fairlie sands, Stranraer, Rough Firth, Auchencarin Bay, Sandyhills Bay.

10. J. Barlee, Ford Brow, Townstal, Dartmouth, Devon.

    - Tresco, Scilly Isles.

11. R. Fowler, Rannock Station, Perthshire.

    - Gourock, Scotland.

12. E.I.S. Rees, Marine Science laboratory, Menai Bridge, Anglesey.

    - N. Wales, Wirral, Conway, Caernarvon Bay, Tremadoc Bay, Mawddach, Davey Estuary. Wexford Harbour, Waterford Harbour, Kerry, Eire.

13. Nelson-Smith A., Univ. College, Swansea, South Wales.

    - South Wales, Galway region.

14. J. Bayes, Sea Salter & Ham Oyster Fisheries laboratories, Whitstable, Kent.

    - Kyle of Tongue, Tremadoc Bay, Llanrhidian Sands, Exmouth, Teignmouth, Poole Harbour, St. Austell Bay, Portsmouth, East Kent; Maplin sands, Wash, Blackwater estuary. Lochars, North Berwick.

15. D.G. Erwin, Ulster Museum, Stranmillis Road, Belfast, N. Ireland.

    - Strangford Lough, Belfast Lough, Red Bay, Donegal Bay, Sligo Bay, Galway Bay.

16. A.J. Collins, Bath Univ. of Technology.

    - Blackwater, Essex. Camel Estuary, Cornwall.

17. D.J. Tighe-Ford, Central Dockyard laboratory, Exposure Trials Station, Southsea, Hants.

    - Portsmouth, Chichester.

18. G. Haslewood, 3 Beach Green, Shoreham-on-sea, Sussex.

    - Adur Estuary, Sussex.

19. S.M. Turk, Marine Census Recorder, Conchological Society of Great Britain.

    - Orkney's, Applecross, Barra, Isle of Skye, Morecombe, Wirral, Jersey, Scilly Isles, Bembridge Isle of Wight, Littlestone, Essex Coast, Wash, N. Norfolk.

20. R. Hammond, 4 Trevellyan Street, Cronulla, New South Wales, Australia.

- Wash and N. Norfolk.

21. A.E. Bowers, Marine Biological Station, Port Erin, Isle of Man.

- Isle of Man.

22. G.E. Newell - (1954) Marine Fauna of Whitstable.

(Ann. Mag. Nat. Hist.) ser. 12. vol 7. p. 321-350.

- N. Kent.

23. D.S. Davis, The Marine Fauna of the Blackwater Estuary and adjacent waters of Essex. The Essex Nat. vol 32 (1) 1967 p. 1-61.

24. S. Lockwood, Lowestoft Fisheries laboratory, Min. A.F.F.

- Humber area.

25. Spooner & Moore (1940) The Ecology of the Tamar Estuary. VI.

- J.M.B.A. 24. p. 283-330.

26. Plymouth Marine Fauna 1967.

- South Devon coast.

B. Legend for distribution of Cerastoderma glaucum (Poiret) around the British Isles.

FH - Forbes & Hanley (1853) reported C. glaucum in the Moray Firth, Scotland, and Great Arran Island, Ireland, as well as in south-east England. The reliability of the former record is debatable.

NH - The Natural History Museum collections of cockles have been examined, and contained specimens from Aberdour, Fife, Scotland (1843); Pevensey Bay and Reculver, N. Kent; Dunwich, Aldeburgh, Suffolk; and Walton-on-Naze, Essex.

NH-DS - Indicates Natural History Museum cockles which are isolated shells and were probably collected as dead shells.

Sites characterised by:-

1. are localities examined by the author in Eire, South Wales and in south-east England in 1968-1969. These sites in the latter case are The Fleet, Weymouth, Dorset; Horsey Island Lake (communicated by P.J. Russell), Alverstoke, Gosport Golf course lagoon, and Hermitage swimming pool, Hampshire; Widewater and Cuckmere Haven, Sussex; Sheerness boating lake, Isle of Sheppey, Kent, New England Creek, Brightlingsea Boating lake, Essex and Shingle street, Suffolk.

DS - Dead shells were also collected at Maldon, Essex and Southwold, Suffolk.

MP - Indicates mixed populations of the two Cerastoderma species.

2. Information communicated by R. Hammond concerning the Salt Hole at Holkam, North Norfolk.

3. Wells-next-the-sea Boating lake. Norfolk - Featherstone (1968).

4. Midrips and Wicks lagoons - Thorpe (1927).

5. Kingsbridge, Devon. Site of original description of C. lamarcki by Reeve (1845).

6. Two sites in North and South Uist recorded by Bowden & Heppell (1968).

Appendix III

Many localities in western Ireland were examined for the presence of C. glaucum. Some were marine, but the majority were fresh water (F.W.). These sites are listed below for the benefit of other workers who may wish to further examine this coastline for the presence of marine lagoons.

Beginning at Newport, Co. Mayo and travelling southwards using the Bartholomew's Revised ¼" maps, sheets 5 and 4, the following localities were visited:-

Drumgarve, Westport, Co. Mayo - marine, loch - C. edule.

Murrisk Abbey, " " " - marine, almost lagoonal - dead shells of C. glaucum?

Roonah Lake, Killeen, " - (F.W.)

Cross Lake, Killadoon, " - (F.W.)

Lake at Rinvyle Hotel, Co. Galway - (F.W.)

Cleggan Bay, Cleggan, " " - (F.W.) C. edule on foreshore.

Aughrusbeg Lake, " " - brackish, almost (F.W.), no cockles.

Steamstown Bay, " " - C. edule on foreshore.

Mannin, Mannin Bay, " " - C. edule.

Toombeola, " " - no cockles located.

Loughaconeera, Flannery Bridge. - no cockles located.

L. Aconeera, Co. Galway - brackish, almost (F.W.), no cockles.

Screeb Bay, " " - C. edule.

Rossaveel, " " - (F.W.).

No suitable sites noted in west Co. Clare, or north Co. Limerick.

Akeragh Lake, Ballyheige, Co. Kerry - (F.W.).

L. Gill, Castlegregory, Dingle, Co. Kerry - (F.W.)

Rossbehy Creek, Nr. Glenbeigh, " " - marine C. edule.

Cahersiveen, Co. Kerry - marine C. edule.

Castletownbere, Barra, Co. Kerry. - Marine C. edule.

Adrigole Harbour, " " - marine C. edule.

Garinish, Glengarriff harbour - marine C. edule.

Toormore Bay, Co. Cork. - marine C. edule

(saline lagoon - no cockles)

Barley Cove, " " - marine C. edule.

(saline lagoon - no cockles)

L. Llyne, " " - marine C. edule.

Carrigillihy lake, Co. Cork. - (F.W.)

Clonakilty, " " - marine foreshore, C. edule.

APPENDIX IV

During the current investigation gymnophallid cercariae or metacercariae were noted in the Cerastoderma between the mantle and the valves, approximately mid-way along the shell. This species was a little smaller than M. minutus, and the excretory granules, in contrast to M. minutus were grey coloured as opposed to black. Diameter, when circular was 0.22 mm. but size was very variable, one very small individual measured 137.8μ x 17.3μ . It also appeared to be more greatly spined than M. minutus. Although this gymnaphallid is thought to be a different species of trematode it was not specifically identified and may represent infective cercariae of M. minutus prior to migration and encystment at the hinge line.

Occurrence of gymnophallid cercaria (or metacercaria?)

In C. edule collected:	at Tollesbury, Essex	2 out of 32
	Wexford Harbour, Eire	4 out of 18
	Southend, Essex	40 out of 140
	Maplin Sands	0 out of 87

From Crouch mixed Cerastoderma population:

Collected on 8.3.69	C. glaucum	1 out of 74
	C. edule	10 out of 80
Collected on 22.4.69	C. glaucum	0
	C. edule	1 out of 82
Collected on 30.6.69	C. glaucum	1 out of 67
	C. edule	2 out of 11
Collected on 14.7.69	C. glaucum	0
	C. edule	1 out of 11
Collected on 19.8.69.	C. glaucum	0
	C. edule	4 out of 20.

APPENDIX V

Comparison of Cercaria mytae (Uzmann, 1952) and Meiogymnophallus minutus (Cobbold, 1859)

The first larval host of the metacercarial parasite of C. edule, Meiogymnophallus minutus is unknown. The normal gymnophallid life-cycle (with the exception of Paratrema homoeotecnum (James, 1964)) involves a first intermediate lamellibranch host, (Stunkard & Uzmann, 1958). Bowers & James (1967) examined many littoral bivalves in an attempt to ellucidate the life cycle, but they do not record the number of each species examined. It may be suspected, by referring to another known gymnophallid life-cycle, e.g. Cercaria dichotoma (Lebour, 1911) that the incidence of infection of the first intermediate host of M. minutus may well be very low. Thus the incidence of the first larval host C. edule, of C. dichotoma, is 0.3% on Llanrhidian sands, South Wales, whereas the incidence of the metacercarial stage in the polychaete Nephtys caeca (O.F. Muller) is 80%, (Bowers, 1965). An incidence as low as 0.3% may well be suspected in the first intermediate host of M. minutus.

Stafford (1912) first found sporocysts and cercaria in Mya cerenaria (L.) from the Gaspe Bay region of Canada. Uzmann (1952) also recorded an infection of a first larval digenean stage in Mya arenaria from Newburyport, on the eastern United States coast, in 3 out of 910 individuals examined. Since then it has subsequently been found in the same host at Boothbay Harbour, Maine at 0.3% incidence, Stunkard & Uzmann (1958) and by Cheng (1967) at Rhode Island. Cercaria myae bears a close resemblance to the metacercarial stage found in C. edule (see comparison

Comparison Table between Cercaria myae & Meiogymnophallus minutus

Description and sizes of Cercaria from Mya arenaria, from Uzmann (1952) & Cheng (1967).	Metacercaria from the cockle C. edule. Description from Bowers & James (1967).
Small, elongate, ovoid furcocercous.	Small, plump, oval and gymnophallid.
Body - 0.12-0.25mm. long. (Stafford (1912) - 0.138 x 0.062)	Body - 0.10 x 0.22mm. long. Smallest (0.13 x 0.08).
Spines - 0.001mm.	Spines - 0.001mm.
Ant. sucker - 0.039-0.052mm. diameter.	Ant. sucker - 0.032-0.042mm. diameter (Mean - 0.039mm.)
Ventral sucker - 0.040-0.046mm. diameter	Ventral sucker - 0.019-0.028mm. diameter (Mean - 0.026).
Pre-pharynx - absent	Pre-pharynx - absent.
Pharynx - 0.020-0.025mm.	Pharynx - 0.016-0.018mm.
Oesophagus - short	Oesophagus - short (0.017mm.)
Intestinal caecae - large with walls composed of polygonal cells, reaching level of ant. $\frac{1}{3}$ of ventral sucker.	Intestinal caecae - 0.061 x 0.031 are short and divergent, reach level just short of ant. border of the ventral sucker in relaxed specimens, and $\frac{1}{2}$ way down sucker in contracted specimens.
Small deeply stained spiral coil maintains a constant lumen between pharynx and oesophagus.	
2 pairs of cephalic glands at post. level of pharynx.	4 pairs of unicellular cephalic glands.
Excretory vesicle - Y-shaped (V-shaped according to Uzmann (1952) with arms recurved round intestinal caecae.	Excretory vesicle - Y-shaped, arms extend to just below oral sucker round intestinal caecae.
Flame-cell pattern - 2 ((2+2+2) + (2+2+2)).	Flame-cell pattern - 2 ((2+2+2) + (2+2+2)).
Body length: oral sucker diameter - 5:1 (from Uzmann's drawings).	Body length: oral sucker diameter - 6:1
Centre of ventral sucker - $^5/_7$ of body length (from Uzmann's drawing).	Centre of ventral sucker - $\frac{3}{5}$ of body length.
Oral sucker: ventral sucker - 50:50.	Oral sucker: ventral sucker - 3:2

table). Mya arenaria would also be a suitable host from an ecological view point, as it occurs in muddy-sand substrates but seldom in pure sand, and it also occurs in estuaries with C. edule. Thus it is tentatively suggested that close examination of English Mya arenaria populations could possibly yield the first larval stage of M. minutus.

REFERENCES

BOWERS, E.A., 1965. Studies on some parasites of sea-birds and molluscs. Ph.D. Thesis, Swansea, Wales.

BOWERS, E.A. & JAMES, B.L., 1967. Studies on the morphology, ecology and life-cycle of Meiogymnophallus minutus (Cobbold, 1859) nov-comb. (Trematoda:Gymnophallidae). Parasitology, Vol. 57, pp. 281-300.

CHANG, T.C., 1967. Advances in Marine Biology, Ed. F.S. Russell. Vol. 5. Marine Molluscs as hosts for symbioses, Academic Press, London and New York.

COBBOLD, T.S., 1859. On some new forms of Entozoa. Trans. Linn. Soc. Lond. Vol. 22, pp. 363-366.

JAMES, B.L., 1964. The life cycle of Parvatrema homeotecnum sp. nov. (Trematoda: Digenea) and a review of the family Gymnophallidae Morozov, 1955. Parasitology, Vol. 54, pp. 1-41.

STAFFORD, J., 1912. On the fauna of the Atlantic coast of Canada. Third report - Gaspe 1905-1906. Contrib. Canad. Biol. 1906-12, pp. 45-67.

STUNKARD, H.W. & UZMANN, J.R., 1958. Studies on digenetic trematodes of the genera Gymnophallus and Paratrema. Biol. Bull. mar. biol. Lab. Woods Hole, Vol. 115, pp. 276-302.

UZMANN, J.R., 1952. Cercaria myae sp. nov., a fork tailed larva from the marine bivalve Mya arenaria. J. Parasit. Vol. 38, pp. 161-164.

APPENDIX VI

Statistical Analyses used in this investigation

1. Test for difference between two sample means

Used to indicate the degree of difference between the normal distributions of shell rib-number is various Cerastoderma populations.

The final tabulated data for the Southend and Roach cockles can be found in tables 4 and 6 in Section V.

The method of calculation for a worked example of the Roach mixed population is shown below.

A random sample of 88 C. edule and 88 C. glaucum have been drawn from the total population.

1. Calculation of the mean

$$\bar{x} = \frac{x}{n}$$

C. glaucum $\bar{x}_1 = \frac{1813.9968}{88} = 20.6136$

C. edule $\bar{x}_2 = \frac{1973.0040}{88} = 22.4205$

2. Estimation of variance

$$V(=s^2) = \frac{(x - \bar{x})^2}{n - 1}$$

C. glaucum $s_1^2 = \frac{138.8648}{87} = 2.1709$

C. edule $s_2^2 = \frac{129.9220}{87} = 1.4934$

3. Estimate standard deviation

$$s = \sqrt{s^2}\ \text{above}$$

C. glaucum $s_1 = \sqrt{2.1709} = \underline{1.473}$

C. edule $s_2 = \sqrt{1.4934} = \underline{1.222}$

4. F test for equality of two variances

To determine if the two distribution curves are almost identical in shape and can therefore be compared:

$$F = \frac{\text{variance } x_1}{\text{variance } x_2} = \frac{s_1^2}{s_2^2}$$

Between C. edule and C. glaucum

$$F = \frac{2.1709}{1.4934}$$

$$= \underline{1.454}$$

The significance of the F value was obtained by reference to tables of F distribution found in 'Biometrets Tables for Statiticians', Table 18. Thus, it was tested whether var. x, was significantly different from var. x_2, with $v_1 = n_1 - 1$ and $v_2 = n_2 - 1$ d.f.

The figure above indicates that the two distributions are not significantly different.

5. t test for difference between the two sample means

$$s^2 = \frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 + 2}$$

therefore

$$s^2 = \frac{87(2.1709) + 87(1.4934)}{174}$$

$$s = 1.353$$

The t test,

$$t = \frac{\bar{x}_1 - \bar{x}_2}{s\sqrt{\frac{1}{n_1} + \frac{1}{n_2}}}$$ is then applied

$$t = \frac{1.8069}{1.358\sqrt{0.0229}} = 8.8271$$

By reference to t tables this figure is highly significant at the 0.001 per cent level.

2. Regression Analysis

For method see - 'Standard Statistical Calculations' by Moore and Edwards, pp. 48-64.

This analysis was used for calculation of oxygen uptake rates (Section VI), and regression lines concerning log. ligament length/log. shell breadth in Section II.

The general method of least mean squares is shown in the following example: Relationship of log. ligament length (mm's) - Log. shell breadth (mm's) in the single Cerastoderma edule population from Whitstable, Kent.

The two linear variables shell breadth mm's (x) and ligament length mm. (y) were converted to logarithms.

$n = 101$

Sum of x, $\Sigma x = 129.7143$ therefore mean of x, $\bar{x} = 1.2843$

Sum of y, $\Sigma y = 82.4262$ therefore mean of y, $\bar{y} = 0.8161$

$\Sigma x^2 = 167.0501$ $\Sigma y^2 = 68.6765$

$\frac{(\Sigma x)(\ y)}{n} = 105.8599$ $\frac{(\Sigma x)^2}{n} = 166.5920$ $\frac{(\Sigma y)^2}{n} = 67.2681$

Corrected sum of the squares for x. $Cxx = \Sigma x^2 - \frac{1}{n}(\Sigma x)^2 = 0.4581$

Corrected sum of the squares for y. $Cyy = \Sigma y^2 - \frac{1}{n}(\Sigma y)^2 = 1.4084$

Corrected sum of the squares for xy.

$$Cxy = \Sigma xy - \frac{1}{n}\Sigma x.\Sigma y = \underline{0.7280}$$

1) The slope of the line b was then calculated:

$$b = \frac{Cxy}{Cxx} = \frac{0.7280}{0.4581} = \underline{+1.5891}$$

(the positive value signifies a positive slope to the regression line)

2) The intercept a on the y-axis obtained from:

$$a = \bar{y} - b\bar{x}$$

$$= 0.8161 - (1.5891)(1.2843)$$

$$= \underline{-1.2248}$$

Thus the equation of the regression line is:

$$y = 1.5891x - 1.2248$$

3) Analysis of variance of regression

Total sum of the squares, Total s.s. = Cyy = 1.4084

Sum of the squares due to regression, reg. s.s. = $\frac{(Cxy)^2}{Cxx}$ = 1.1569

About regression (residual) s.s. = Total s.s. - reg. s.s.

therefore resid. s.s. = 1.4084 - 1.1569

= 0.2515

From the above data an Analysis of Variance table was tabulated

Source	s.s.	d.f.	M.S. = $\frac{\text{s.s.}}{\text{d.f.}}$	M.S.R.
Due to regression	1.1569		1.1569	462.76
Residual	0.2515	(n - 2)99		
Totals	1.4084			

The Mean Square Regression (M.S.R.) or F- test, compares the mean squares due to regression with the residual mean squares. Reading on F - tables, where v_1 = due to regression d.f. = 1, and v_2 = Residual d.f. = n - 2 - 1.

The above example is shown to be highly significant at the 0.1 per cent level. The above f test was only added for completeness, the correlation co-efficient r below being used for indicating the significance of the regression fit.

The correlation co-efficient r was obtained from:

$$r = \pm \frac{\text{Due to reg. s.s.}}{\text{Total s.s.}}$$

$$= \pm \frac{1.1569}{1.4084} = \underline{0.0963}$$

The correlation co-efficient takes the same sign as b. The significance of r was determined by comparing value of r against tables of r (Biometrika tables for staticicians Vol. 1. - Cambridge University Press, 1954) Table 13, $v = n - 2$ d.f.

The value above is highly significant at the 0.01 per cent level indicating a good regression fit.

95% confidence limits about regression lines

The 95% significance point of $1- (1-'_{95})$ was obtained from t distribution tables (Moore and Edwards, Table 2, p. 110) with $v = n - 2$ d.f.

For large samples (> 30) the approximate formula

$$D_{95} = 1-'_{95} \times Sr$$

where $Sr = \sqrt{\text{resid. M.S.}}$

Reprinted from THE ESSEX NATURALIST, *Vol. 32, Part 3, 1969.*

Ecology of the cockle *Cardium glaucum* Brugière*

By C. R. BOYDEN

(Queen Mary College, London)

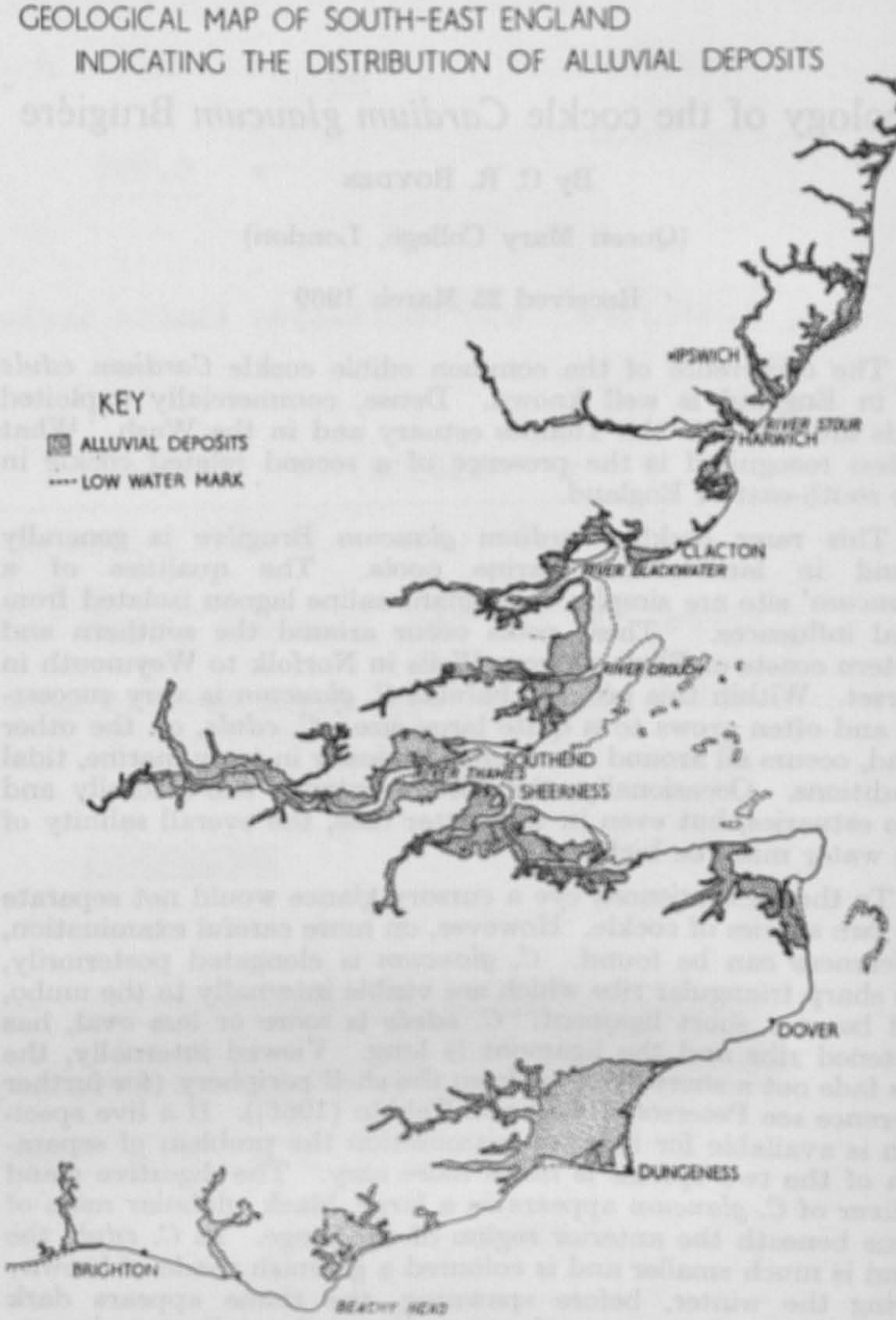
Received 25 March 1969

The occurrence of the common edible cockle *Cardium edule* L. in England is well known. Dense, commercially exploited beds are found in the Thames estuary and in the Wash. What is less recognised is the presence of a second related cockle in the south-east of England.

This rarer cockle, *Cardium glaucum* Brugière is generally found in land-locked marine pools. The qualities of a '*glaucum*' site are simple; a stagnant saline lagoon isolated from tidal influences. These pools occur around the southern and eastern coasts of England from Wells in Norfolk to Weymouth in Dorset. Within this peculiar habitat *C. glaucum* is very successful and often grows to a quite large size. *C. edule,* on the other hand, occurs all around our shores, typically in truly marine, tidal conditions. Occasionally, the species extends sub-littorally and into estuaries, but even in this latter case, the overall salinity of the water must be high.

To the inexperienced eye a cursory glance would not separate the two species of cockle. However, on more careful examination, differences can be found. *C. glaucum* is elongated posteriorily, has sharp triangular ribs which are visible internally to the umbo, and bears a short ligament. *C. edule* is more or less oval, has flattened ribs and the ligament is long. Viewed internally, the ribs fade out a short distance from the shell periphery (for further reference see Peterson (1958) and Tebble (1966)). If a live specimen is available for internal examination the problem of separation of the two species is made more easy. The digestive gland or liver of *C. glaucum* appears as a large, black, globular mass of tissue beneath the anterior region of the hinge. In *C. edule* the gland is much smaller and is coloured a greenish shade of brown; during the winter, before spawning, the tissue appears dark green, whereas in summer the tissue is most usually pale brown. The organ is not as discrete or globular in appearance as it is in *C. glaucum.* This internal character has proved most useful in separating the two kinds of cockles. With additional knowledge of the shell shape and habitat, positive identification is possible.

*Nomenclature follows Mars (1951), and Russell (Ph.D. thesis, London. 1969).



What is the relationship of *C. glaucum* to *C. edule*? Eisma (1965) regards *C. glaucum* (as *C. lamarcki*) as a variety of *C. edule*, whilst Mars (1951) and Petersen (1958) consider the two cockles as separate species; an opinion adopted here because of the anatomical and ecological differences. *C. edule* is recognised as a variable species, and some thirty-five varieties have been

described (Mars, 1951 and Grossu, 1961). Even around our shores *C. edule* collected from different sites can often be recognised by their local shell characteristics. Thus Southend cockles can be separated from those of the estuarine River Crouch, and Weymouth, South Wales and Anglesey cockles are also identifiable by their shell shape. In sites where the environment is particularly 'stressed', e.g. sedimentation tanks of power stations, the *C. edule* respond to the conditions by exhibiting globular 'odd' shaped shells. Therefore *C. edule* is a very variable species as regards shell shape and is able to produce many 'ecotypic varieties' which should not be confused with specific differences. However, on the shore, there is not a range from *'edule'* type to *'glaucum'* type, so the occurrence of *C. glaucum* in pools seems to be independent of the presence of *C. edule* on the adjacent shore. This does not mean to say that *C. glaucum* cannot occur on the shore for very occasionally isolated individuals are found between tide marks. Could the larvae from these animals spread the species into newly formed pools? The apparent rarity of these individuals would probably discount such a hypothesis.

It is interesting at this stage to examine the European distribution of the two cockles. *C. edule* extends southwards along the Atlantic coasts of France and Spain, and northwards to Holland and Denmark. It is also found in the approaches to the Baltic where oceanic effects are still evident, e.g. the Kattegat shores of Sweden and Denmark (G. Hopner-Peterson, personal communication). *C. glaucum* on the other hand is found in the inner Baltic (Petersen, 1958) and the Mediterranean (Mars, 1951). Both seas have a very small tidal rise and fall, thus the cockles remain permanently submerged in basically still water. The lagoon *'glaucum'* sites found throughout southern England are miniature versions of these non-tidal seas. The habitat of this 'not-so-common' cockle is not so strange or unusual as first appears.

Petersen (1958) in discussing the occurrence of *C. glaucum* in the Baltic Sea, considers this cockle to be a brackish water form. However, the cockle occurs in the Mediterranean where the salinity is high. Certainly around our coasts *C. glaucum* is found in pools where there is brackish water. The lowered salinity character of the pools may not be essential, continual submersion in stagnant saline water being the primary requirement of the cockle.

In the very recent geological history of England, saline or brackish water lagoons were probably much more common than they are at the present day. The region of alluvium shown in the geological map of S.E. England (see Fig. 1) represents original areas of marshland where lagoons may well have been abundant. The area of modern marsh and saltings is much lower and is mainly retained behind sea defences. Very few modern marshes contain water of sufficient salinity to harbour *C. glaucum*. With the advent of sea walls in about the thirteenth century (Grieve, 1959) the number of potential *C. glaucum* sites would gradually

have become reduced. Storm surges are well known and the disastrous flooding of 1949 and 1953 were the result of such phenomena. When spring tides concur with deep depressional activity over the North Sea exceptional high tides are produced, with the resultant breaking of sea defences. These storm surges are documented as far back as 1552 (Brown, 1927). The alluvial deposits close to the coastline indicate regions where the sea, at spring tides and especially during storm surge conditions, was driven inland to inundate the marshes. Vast drowning of marshland and replenishment of lagoons with saline water is likely to have occurred with the concurrent distribution of the cockle from lagoon to lagoon. J. T. Greensmith and E. V. Tucker (personal communication) have located a bed of *C. glaucum* shells now some two miles inland north of Burnham-on-Crouch, Essex. These shells are regarded as a life assemblage and are found in the bank of a modern drainage ditch. The creation of sea defences no doubt effectively reduced the number of, and isolated, separate lagoon populations of *C. glaucum.*

The most rational approach to the presence of *C. glaucum* round our south-eastern shores would be to consider the sites we know at present as remnants of a much wider distribution. With further reclamation and fresh water canalisation, this rare cockle will undoubtedly become even rarer; but not, I hope, before marine biologists recognise its specialised existence as one of the few lamellibranchs to invade and remain in stagnant brackish water.

References

Brown, E. (1927). An Essex Island Parish. *Essex Review*, **36**: 176.

Eisma, D. (1965). Shell-characteristics of *Cardium edule* L. as indcators of salinity. *Netherl. J. Sea. Res.*: 493-540.

Grieve, H. (1959). The great tide. Essex County Council.

Grossu, A. V. (1961). Variatiile lui *Cardium edule* L. *Marea Neagră Hidrobiol.*, **3**: 177-91.

Høpner-Petersen, G. (1958). Notes on the growth and biology of the different *Cardium* species in Danish brackish water areas. *Medd. Komm. Pra. Danm. Fisk-og Havunders* (N.S.), 11, **22**: 1-31.

Mars, P. (1951). Essai d'interpretation des formes generalement groupees sous le nom de *Cardium edule* L. *Bull. Mus. Nat. Hist. Marseille*, **11**: 1-31.

Robinson, A. H. W. (1953). The changing coastline of Essex. *Essex Nat.*, **29**: 79-93.

Tebble, N. (1966). *British Bivalve Seashells*, 97-108, British Museum (Natural History).

...9

...e 1969

Compiled by: P. E. ...
32 Chel... C...
Chelsea Emb... ...
London, S.W.3.

Produced by THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELA...

SOME NOTES CONCERNING CERASTODERMA LAMARCKI (REEVE)

There is considerable interest in Conchological circles in the ec... ...rastoderma (Cardium) lamarcki. In the December 1968 Newsletter, ... Featherstone described a 'lamarcki' site at Wells-next-the-Sea, Norfol... ...and suggested ideas for the origin of the habitat. I have been engag... ...conducting research into this cockle and have some further ideas concern... the relationship of the common edible cockle Cerastoderma (Cardium) edule Linné to Cerastoderma lamarcki.

The 'C.-edule-lamarcki' genetic complex of cockle exhibits many different shell shapes and some 35 varieties have been described by ... 1951, and Grossu 1961, especially from the Mediterranean area. Even ... our shores, C. edule collected from different sites can often be rec... by their local shell characteristics. Thus Southend cockles can be s... ...d from the River Crouch estuarine C. edule. Weymouth, South Wales ... Anglesey cockles are also identifiable by their shell shape. In sites ... the environment is particularly 'stressed', e.g. sedimentation tanks of ... ...ctions, the C. edule respond to the conditions by exhibiting ... ...'odd' shaped shells. Therefore C. edule is a very variable spec... ...regards shell shape and is able to produce many 'ecotypic varieties', (environmental types), which should not be confused with specific differences.

However, the two closely related species of cockle C. edule L. and C. lamarcki REEVE can be recognised in British waters. To the inexper... ...ye, these two cockles can be very difficult to separate, but if a live ...ecimen is available the problem is eased. When the valves are sep... ...very obvious internal difference becomes apparent. The digestive ... ...iver of C. lamarcki appears as a large, black, globular mass of tis... ...th the anterior region of the hinge. In C. edule the gland is sma... ... is coloured a shade of green or brown. In the winter the tissue ... ...a green, whilst during the summer months this colour is often cha... ...le brown. The organ is not as discreet or globular in appearance ... ...n C. lamarcki. This internal character has proved most useful in ... ...ration of the two cockles from around our coasts. With additional ... ...e, of the habitat and shell shape, positive identification is pos... ...the amateur.

...n 1965 regards C. lamarcki simply as a variety of C. edule, ... and Petersen 1958 consider the two cockles as separate speci... ...e conclusions have been drawn from consideration of shell chara... ...cs which have been fully elucidated by Petersen 1958, Turk 1964 ... ...le 1966. C. lamarcki is elongated posteriorly, has sharp trian... ...which are visible internally to the umbo and bears a short liga... ...du is more or less oval, has flattened ribs and the ligament is ... ...e internally, the ribs fade out a short distance from the shell ...plum.

...e lake at Wells, Norfolk, described by Featherstone 1968 is a ...cal example of what can be regarded as a 'lamarcki' habitat. The ...ities of such a site are simply as follows: a stagnant saline lago... ...ly from marine influences. Such sites occur quite frequently arou... ...south-east coast of England, e.g. Brightlingsea boating lake; New ...rk, Foulness; Sheerness boating lake, Sheppey; Widewater, ...ng; Hermitage near Portsmouth; The Fleet at Weymouth, Dorset, to ... ...a few of the better examples. The lagoon feature of the vast majorit...

'lamarcki' sites must not be regarded as a retrograde step from [illegible] shore. Within this specialised habitat C. lamarcki is very successful and often grows to a quite large size. However, what is the relationship between C. edule and C. lamarcki?

C. edule occurs all around our shores, typically in truly marine tidal conditions. Occasionally, the species extends sub-littorally and into estuaries, but even in this latter case the overall salinity of the water must be high. This cockle extends southwards along the Atlantic coasts of France and Spain, and northwards to Holland and Denmark. It is also found in the approaches to the Baltic where oceanic effects are still evident, e.g. the Kattegat shores of Sweden and Denmark, Petersen 1968.

C. lamarcki is found in the inner Baltic and the Mediterranean. Both seas have a very small tidal rise and fall, thus the cockles remain permanently submerged in basically still water. The lagoon 'lamarcki' sites found throughout Southern England are miniature versions of these non-tidal seas. The habitat of this 'not-so-common' cockle is not so strange or unusual as first appears.

How can the distribution of C. lamarcki in isolated pools be explained? Featherstone 1968 suggests that C. lamarcki could be a recently evolved form of C. edule. Although C. edule is a very variable species there is not a range from 'edule' type to 'lamarcki' type on the shore, so this explanation is unlikely to be valid. Very occasionally, true C. lamarcki are picked up on the open shore. I have found three such individuals at Whitstable, Kent; Tollesbury, Essex; and at Hermitage near Portsmouth. G. Pickett of Burnham Shellfish Laboratories also found such a specimen at Poole, Dorset. Could the larvae from these isolated individuals spread the species into newly formed pools? The apparent rarity of these individuals would probably discount such a hypothesis. Considering C. lamarcki's Northern European distribution, Petersen, 1958, regards this cockle as a brackish water species. In the very recent geological history of England, brackish water lagoons were probably much more common than they are at the present day. With the advent of sea walls in about the thirteenth century (Grieve, 1959), the number of potential C. lamarcki sites would gradually have become reduced. Greensmith, J.T., and Tucker, E.V., 1969, have located a bed of C. lamarcki shells some two miles inland north of Burnham-on-Sea, Essex. These shells are regarded as a life assemblage and are found in the bank of a modern drainage ditch. The creation of sea defences effectively reduced the number of, and isolated, separate lagoon populations of C. lamarcki.

I suggest that the most rational approach to the question of the occurrence of C. lamarcki round our shore would be to consider the sites we know at present as remnants of a much wider distribution. With the further reduction of suitable 'lamarcki' sites owing to reclamation and fresh water canalisation the 'not-so-common' cockle will I feel in the future become even rarer than it is at present.

Bibliography:

Lisma, D. 1965: Shell-characteristics of Cardium edule L. as indicators of salinity. Neth. Jour. of Sea Res. 2, p.493-540.

Featherstone, A. 1968: Abraham's Bosom. The Conch. Newsletter No. 27, p.66-8.

Grieve, H. 1959: The Great Tide. Pub. Essex County Council.

Greensmith, J.T., Tucker, E.V. 1969: (Personal communication).

Ionesu, A.V. 1961: Variatiile lui Cardium edule L. în Marea Neagra. Hydrobiol. Vol. III, p.177-91.

Spaer Petersen, G. 1958: Notes on the growth and biology of the different Cardium Species in Danish brackish water areas. Medd. Komm. fra. Danm. Fisk-og Havunders. N.S.II, 22, p.1-31.

Petersen, G. 1968: (Personal communication).

Ars, P. 1951: Essai d'interprètation des formes généralement groupées sous le nom de Cardium edule L. Bull. Mus. Nat. Hist. Marseille, 11, p.1-31.

Lockett, G. 1968: (Personal communication).

Tebble, N. 1966: British Bivalve Seashells. Pub. Nat. Hist. p.97-108.

Turk, S.M. 1964: The Conch. Newsletter No. 10, p.61.

C. R. Boyden, B.Sc. (Queen Mary College)

FLEET: A BRACKISH WATER HABITAT

In arranging to go to Fleet, Dorset, for a week's holiday, I must confess that I quite forgot the remarks in the Marine Recorder's annual report in February 1968, in which Mrs. Turk appealed for more information about this locality; so conchologically speaking, it was pure coincidence which took us there rather than a spirit of helpfulness. In the upshot, the area proved to have quite a lot of interest.

The Chesil Bank is a magnificent storm beach which stretches seventeen miles from Burton Bradstock to Portland; for most of its length it is about a hundred yards wide and fifty or sixty feet high, composed entirely of pebbles varying in size from that of a pea at the west end to flattened boulders about nine inches across near Portland. The source of the pebbles was a series of ancient drowned river terraces on the Devon and Cornwall coasts.

The Bank leaves the coastline over about half its length, thus enclosing a lagoon which stretches from Abbotsbury to Portland, and varying in width up to about a mile across. It forms a quite unusually stable brackish water environment, not much subject to the introduction of any outside species. The streams entering the lake are few and small, and on the seaward side, the Bank is quite without littoral life. Occasional stray shells undoubtedly get blown or thrown over the Bank from time to time, and we found Littorina littorea, L. littoralis, Crepidula fornicata and cuttlefish pens: all were knocked about however, and there is no evidence that any of them live in the lagoon, the waters of which are scarcely brackish - that is, they may be described as fresh but with a distinctly salty taste. The tide rises and falls between one and two feet, presumably by seepage through the pebble bank, and the lagoon is very shallow, of the order of four to six feet in most places, with a bottom of soft mud. Some sewage effluent enters, but the area is lightly populated.

Apart from blanket-weed, practically the only vegetation seen anywhere was eel grass, Zostera marina and Z. nana, these being the main reason for the existence of the swannery at Abbotsbury, established by the swans themselves prior to the fourteenth century. It was noticeable that on the Bank at points opposite the entry of small streams low bushes had established themselves among the pebbles near the water's edge, and scattered plants such as samphire, sea pink and campion were growing.

As with most brackish localities, molluscan species were few but the numbers of the individuals enormous. The smooth variety tenebrosa of Littorina saxatilis in a confusion of shades and sizes swarmed at the water's edge in hordes, freely mixed with the shells, mostly dead, of Mytilus membranacea* and Abra tenuis, and a few dead or dying specimens of Cardium lamarcki. Of Hydrobia ventrosa, previously reported from the lake, we saw nothing in spite of several days' searching in various spots, although we did not get to the mouths of any of the little streams, at some of which they no doubt occur. The only other mollusc seen was the rather large-spotted Akera bullata, living in profusion, but only on the western or inland side, where it was no doubt better sustained by the saltier water coming through the Bank. The species was dwelling happily in a few inches